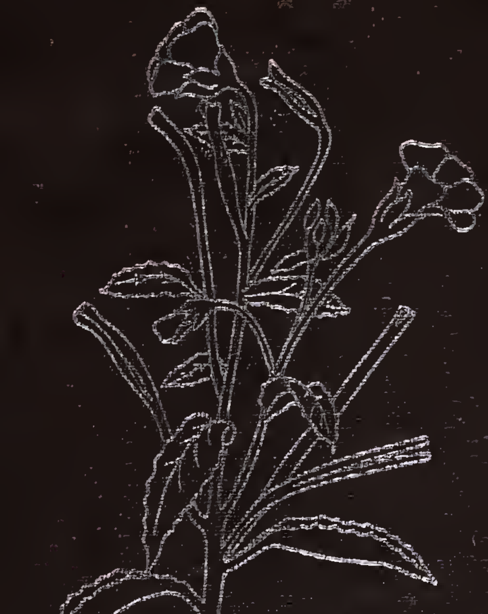
General Botany



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General Botany

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General Botany

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Editor's Preface

While retaining the selection and most of the presentation in the third German edition, I have made every effort to check the accuracy of the English translation and of the basic concepts presented. A conscious attempt has been made to add definitions and to superimpose an outline that will aid the reader in grasping developmental concepts at the cellular and tissue level. This is not a textbook that aims to present a detailed and comprehensive treatment of all of botany. Rather, it is a careful selection of fundamental problems with emphasis on development—its cytology, physiology, and genetics.

Dr. Wilhelm Nultsch wrote this book for a one-semester course. The broad coverage of this text does not differ substantially from that of the first semester of a two-term General Biology course and not all from the in-depth coverage of the one-semester course on Principles of Botany, both given at Rutgers University.

There is a section on the molecular constitution of organisms, and important chemical groups and compounds are discussed in their biochemical context so that the complicated chemical reactions in living organisms will be more intelligible. Protoplasm is discussed in terms of chemical constituents, ultrastructure, and organelles, leading to single cells or colonies and their growth and differentiation. The student is then introduced to the various organizational and evolutionary forms of cells up to the seed plants and their structures and associated processes. This is followed by chapters on the respiration of materials and energy transformations, water and salt balance, translocation, energy-procuring and synthetic processes in autotrophic plants, nitrogen metabolism, and heterotrophy. Next, reproduction, genetics, and control of development are discussed in sequence, recognizing the interaction and unification of these processes. Microorganisms are often chosen as examples in discussing physiological and genetic problems simply because most modern research in cell biology is based upon microorganisms. One chapter deals with motion phenomena in plants. The principles of energy flow, not in the context of an ecosystem, and carbon and nitrogen cycles, but in the sense of biogeochemical cycles, are explored. Levels of organization in cells, organs, and individual organisms are emphasized. In ecology, we are more concerned with populations, communities, and ecosystems and their homeostatic mechanisms.

Emphasis, then, is on the developmental concepts at the cell and organ level. The thorough treatment of both plant structure and function should clarify the most modern aspects of plant growth and differentiation and suggest possible genetic control mechanisms. The emphasis on chemical constituents, ultrastructure, and organization of cells and the chapter on motion phenomena in plants illustrate the essential similarities of plants and animals.

For the student seeking clarification of any topic covered in the text or for the student who may be particularly interested in a topic given only general treatment, a selected bibliography has been included at the end of each chapter.

At the end of the book I have added two summaries to the short taxonomic survey in which the genera and species mentioned in the text are listed under their proper scientific classification. The summary on evolution is organized under history, evidence for evolution, methods, and alternation of generations, with selected readings for each section. The one on ecology seeks only to present to the reader a very comprehensive list of readings under headings designed to show the broad, unifying concepts of ecology. Since the coverage in most texts is not adequate (especially if ecology is being emphasized) and the field is changing so rapidly, I am presenting selected outside readings to complement any lectures that may be presented.

The proper frame of reference for a reading of this textbook may be provided by quoting from Marcus Aurelius Antoninus (AD 121–180):

> Observe always that everything is the result of a change, and get used to thinking that there is nothing nature loves so well as to change existing forms and to make new ones. . . .

JAMES E. GUNCKEL

Author's Preface

There is at present no shortage of comprehensive textbooks of botany and general botany, but the lack of a short introductory text for teaching purposes is making itself increasingly obvious. A book is required that will provide students with an introduction to the fundamental problems of this area of biology.

The object of this textbook is to fill this gap. It is based on the general botany lectures given for a number of years at the University of Tübingen. Certain aspects of the subject, such as morphology, anatomy, and histology, are treated more thoroughly in the book than they were in the lectures, because students of natural sciences, e.g. microbiologists, biochemists, and pharmacologists, have a need for a knowledge of general botany. The book should also serve as an introductory or at least supplementary reading for all biologists. Many problems are raised which are either not discussed at all in textbooks of botany or are treated only peripherally.

The results and problems of general biology as they relate to cytology, physiology, and genetics have been emphasized, while other interesting problems—of ecology, evolutionary history, etc.—which are new, and rapidly changing areas have been briefly treated. For the same reasons, microorganisms have often been chosen as examples in the discussion of physiological and genetic problems, which does not mean that another object would not have often been equally suitable for the purpose.

Since experience shows that students of general botany are rarely equipped with a knowledge of chemistry and physics necessary for the understanding of life processes, the book begins with a short chapter on the molecular constitution of plant organisms. All the important compounds and classes of compounds, whose knowledge is assumed in subsequent chapters, are defined and explained. Many cross-references are provided, and with their aid it is possible to find information on the most important properties of the various compounds mentioned later in the text. It must be emphasized that this chapter cannot replace a thorough study of the relevant chemical and biochemical textbooks. On the contrary, it should stress the importance of adequate chemical and biochemical background for the study of biology and induce the student to study these subjects more thoroughly.

As progress in the analysis of life processes continues into molecular dimensions, it becomes less and less possible to avoid discussion of the chemical reactions underlying life processes. In any case, the complicated chemical reactions taking place in living organisms will not become more intelligible if one desists from a treatment in terms of formulas. The beginner must appreciate that chemical formalism is a superb simplification, making it possible to discuss the cell processes. For this reason many of the chemical compounds and reactions discussed in this book are illustrated by the corresponding structural formulas and equations. Of course, this does not mean that these formulas and equations have to be learned by rote. The extent to which their knowledge is required must be decided by the instructor.

The discussion of the structure of protoplasts and their cellular organization leads directly from the single cell along the various organizational forms to the Tracheophyta and their structure. This is followed by chapters on the metabolism of materials and energy transformations. It might appear unusual that the discussion of metabolism precedes that of reproduction, but this arrangement has the advantage that reproduction, genetics, and development can be discussed as one unit. The chapter on reproduction can in any case be read before the one on metabolism. The last chapter deals with a review of motion phenomena of plants. At the end of the book there is a short taxonomic survey in which the species and genera mentioned in the text are listed under their scientific names.

At a time when it is hard for a single individual to keep up with developments in his own specialized field, it is a difficult decision to embark on a comprehensive review of even selected topics in general botany. The opinions on individual questions are often liable to change rapidly, and it is not always possible to follow these changes at once, as it is difficult to distinguish between what can be regarded as proved and what is only the opinion of a single researcher or a group of researchers. Every author must therefore rely increasingly on the participation and criticism of his colleagues. I am especially indebted to Professor Bünning for reading the manuscript and for his suggestions and criticisms. Thanks are also due Professors Haupt, Haustein, Mägdefrau, and Mohr for many critical suggestions and discussions.

I am grateful to Professor Drews and to Drs. Giesbrecht and Könitz for original electron micrographs, to Professor Mägdefrau for his permission to use his block diagram, and to Professor Oehlkers for permission to reprint some of the diagrams from his book "Das Leben der Gewächse."

All diagrams have been redrawn, even when taken over from older editions; most of them have also been slightly altered. Three-dimensional representation has been favored wherever it seemed suitable. I am indebted to Herr K. H. Seefer for careful execution of the diagrams and to Herr J. Paland for the equally painstaking drawing of formulas.

WILHELM NULTSCH

Chapter 1

The Molecular Constitution of Plants

All living organisms are built up from molecules which in turn consist of atoms. The atoms themselves can be broken down into smaller units, such as protons, neutrons, and electrons, though such decomposition would alter the chemical nature of the atoms. It is obvious, therefore, that every change in the molecular or atomic structure of the body substances must affect the vital processes of the organism and, conversely, that all physiological processes must stem from certain biochemical or biophysical phenomena. If we are to gain a true understanding of an organism and its life processes, we have to track these down to molecular or even to atomic dimensions.

This problem is dealt with by molecular biology which has developed into an autonomous scientific discipline in the course of the last decade.

The Elemental Composition of Plants

The elemental chemical analysis of a great variety of plants has shown that the vegetative plant body consists essentially of the following elements: the nonmetals—carbon C, oxygen O, hydrogen H, nitrogen N, sulfur S, and phosphorus P; and the metals—potassium K, calcium Ca, magnesium Mg, and iron Fe.

Many elements other than those just mentioned can certainly be detected in plants, some in large quantities, such as sodium Na, silicon Si, and chlorine Cl, and some only in very small quantities, e.g., copper Cu, molybdenum Mo, or boron B. Practically all elements have in fact been found to occur in plants, although this, of course, does not imply that they are all essential to plant life. Some of them are characteristic components of certain ecotypes, i.e., of plants adapted for special habitats, such as the element sodium in halophytes. Some other elements represent only ballast material without playing any specific role in metabolism. The importance of an element for the plant does not depend on the proportion in which it is present in the plant material, as shown by the so-called trace elements. As their name implies, these occur in plants only in traces; they are nevertheless essential, and their deficiencies result in serious physiological damage (see p. 189).

The percentage contribution of the various other elements to the plant material also varies significantly. The dry matter left afer the removal of water consists mainly of the nonmetals C, O, H, N, S, and P.

Carbon

Carbon is the predominant element in plants, both in quantity and importance. This special significance is due mainly to the ability of carbon atoms to combine with each other to form long chains, an ability not shared to this extent by any other element. This allows the formation of large molecules, which is an essential prerequisite for the formation of an unlimited number of various materials and for the specificity of the substances in the living organism (see pp. 7, 15).

Carbon is tetravalent in all its compounds, i.e., a carbon atom can combine with four monovalent atoms, for example, with four hydrogens to form methane CH_4. The tetravalence is due to the fact that carbon has four valence electrons, and can therefore accept only another four to make up a shell of eight external electrons; such a shell, a so-called inert gas configuration (octet), is extremely stable. When the carbon atom combines with another element, such as hydrogen in the case of methane, its external shell of electrons is completed by the electrons of the other element (Fig. 1.1). Each hydrogen atom possesses only one valence electron, so that four hydrogen atoms combine with one carbon. The carbon

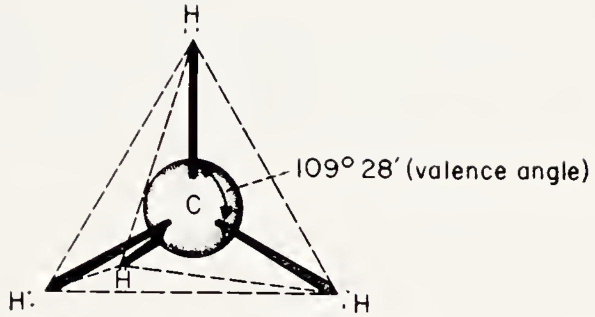
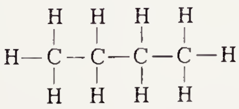


FIG. 1.1. The tetrahedral model of the carbon atom, combining with hydrogen (• H) to form methane.

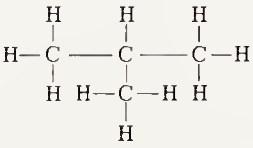
shares one electron pair with each hydrogen, and since the innermost shell (the K-shell) can only carry two electrons, the electron shells of the hydrogen atoms are also completed. Each shared electron pair corresponds to a single bond, i.e., one valence. Shared electron pairs or valences are commonly represented by dashes when the formula of a compound is written out; this symbol will be retained in this book. Bonds of this type are referred to as covalent bonds. Such bonds are very strong, being of the same order of strength as the so-called ionic bonds between singly and oppositely charged ions such as Na^+ and Cl^-. Covalent and ionic bonds are therefore also referred to as primary valences.

A similar bonding situation arises when carbon atoms combine to form chains. Since every carbon combines with only two other carbon atoms when forming continuous (n- = normal) chains, two electrons remain unpaired on each atom; these two free valences can be utilized by other elements, such as hydrogen. Compounds of this type are known as hydrocarbons. The first members of the series are methane, CH_4; ethane, C_2H_6; propane, C_3H_8. (The members have the general formula C_nH_{2n+2}.) As the number of atoms of carbon and hydrogen increases beyond propane (C_3H_8) to butane (C_4H_{10}) the possibility arises of a different structural configuration (e.g., isobutane with a T-shaped arrangement). Such substances, which have the same molecular formula but different structural formulas, are known as *isomers*. Each of the butanes is an isomer of the other.



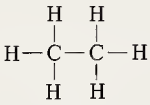
$$\begin{array}{ccccccccccc} & & H & & H & & H & & H & & \\ & & \vert & & \vert & & \vert & & \vert & & \\ H & - & C & - & C & - & C & - & C & - & H \\ & & \vert & & \vert & & \vert & & \vert & & \\ & & H & & H & & H & & H & & \end{array}$$

n-Butane



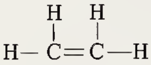
Isobutane

The carbon atoms can also form rings of three, four, five, six, or more members (isocyclic rings). Rings containing one or more atoms other than carbon are said to be heterocyclic (see p. 1). Finally, two carbon atoms can also be linked by single, double, or triple covalences.



$$H-\overset{\overset{H}{|}}{\underset{\underset{H}{|}}{C}}-\overset{\overset{H}{|}}{\underset{\underset{H}{|}}{C}}-H$$

Ethane



$$H-\overset{\overset{H}{|}}{C}=\overset{\overset{H}{|}}{C}-H$$

Ethylene

$H-C\equiv C-H$

Acetylene

The four valences of the carbon atom do not lie in the same plane but are so disposed that joining the ends of the four valence bonds yields a regular tetrahedron; the carbon atom lies at the center of this tetrahedron (Fig. 1.1). As a consequence carbon chains are not straight but arranged in a zigzag pattern, corresponding to the valence angle (Figs. 1.1 and 1.2). The abundance of 5- and 6-membered carbon ring systems is also due to the ease with which such rings are formed as a consequence of the magnitude of the valence angle (Fig. 1.3), while all smaller ring systems are subject to a certain strain. Double and triple bonds are more reactive than single bonds.

The Formation of Molecules

As has already been mentioned, molecules can be formed from atoms of one or several different elements which enter into mutual combinations to fill their electron shells. Frequently this occurs only when the atoms are in higher energy states having absorbed external energy. Such energy can be supplied by radiation, electric discharges, and heating.

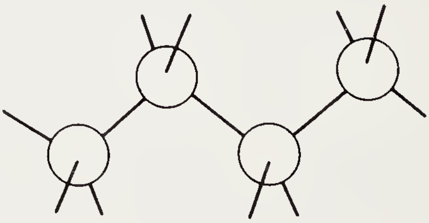


FIG. 1.2. A chain of carbon atoms, in zigzag array corresponding to the valence angle in Fig. 1.1.

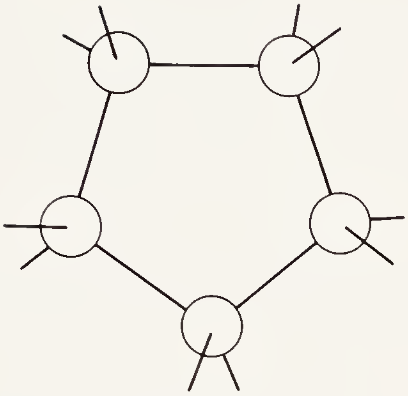


FIG. 1.3. Five-membered, strain-free ring of carbon atoms.

When an atom collides with a quantum[1] of sufficiently high energy, its energy status can change in various ways depending on the energy content of the quantum. One of the electrons of the target atom may be transferred to a higher shell, i.e., to a higher energy level (Fig. 1.4). This process is referred to as excitation. Alternatively, an electron may be ejected completely from the atom in a process called *ionization* (Fig. 1.5). The electron may receive the whole energy of the quantum and will then, as a photoelectron, excite other atoms. Atoms excited in this manner are very reactive and can form molecules by reacting with each other or, when they already form part of a molecule, can cause it to undergo further reactions or disintegration (formation of free radicals). Such excited states feature in many biochemical and physiological processes, and are necessary for the formation of organic molecules from inorganic ones. This process is, in turn, essential for the formation of living organisms and must have occurred at some time in the past on the Earth.

As to the fundamental question of the origin of life, it is irrelevant whether this process has actually occurred on Earth or on another planet from which, according to Arrhenius' theory spores have reached and infected the Earth. This merely transfers the problem to another locality. When the Earth's crust cooled sufficiently, reactions between the avail-

---

[1] A light quantum or a photon ($h\nu$) is the smallest absorbable amount of electromagnetic radiation; a molecule either absorbs a whole quantum or none. The symbol h represents Planck's constant and ν the frequency of the radiation. The energy of a quantum is $E = 12{,}403\ \mathrm{eV}/\lambda$; E is expressed in electron volts (eV) and λ is the wavelength in Å. The energy of a quantum of electromagnetic radiation is therefore inversely proportional to the wavelength. The energy of photons in the visible region of the spectrum is in the range of 40–70 kcal/mole. One mole of photons is also referred to as 1 Einstein (1E).

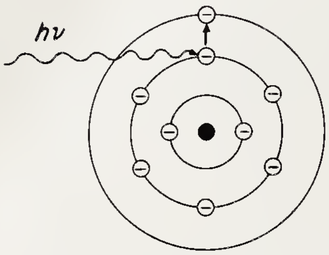


FIG. 1.4. Excitation: One of the electrons of an atom is raised to a higher energy level by the absorption of energy.

able elements must have occurred. Initially, small molecules like ammonia (NH_3), methane (CH_4), and water (H_2O) must have been produced in these reactions, followed later under different conditions by the synthesis of larger "organic" molecules. Originally the necessary excitation energy for this could have been of thermal nature, but the main contribution must certainly have come from solar or nuclear radiation and from the electric discharges in thunderstorms.

The basic possibility of the formation of organic compounds in this way has been demonstrated by interesting experiments carried out by Miller, Urey, Calvin, and their co-workers. If a reducing (oxygen-deficient) atmosphere consisting of methane, hydrogen, ammonia, and water is placed in a closed system (Fig. 1.6) and exposed to electric discharges or to high energy radiation, the reaction products will consist not only of simple carbon chains like acetic acid ($C_2H_7O_2$), lactic acid ($C_3H_6O_3$), and succinic acid ($C_4H_6O_7$), but also of the amino acids glycine (NH_2-CH_2COOH), alanine ($C_3H_7O_2N$), glutamic acid ($C_5H_9NO_4$), and others, which are the structural elements of protein molecules. The first step from the inorganic material to the organic carbon compounds can now be realized experimentally under conditions resembling those that prevailed in the presumed primeval atmosphere.

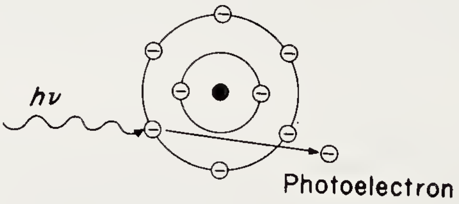


FIG. 1.5. Photoelectric effect: The incident proton transfers the whole of its energy to one of the electrons of the atom; this photoelectron leaves the energy sphere of the atom. (Adapted from Fritz-Niggli.)

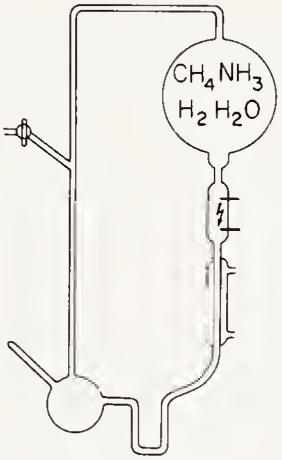


Fig. 1.6. Apparatus for the production of organic compounds in a "primeval atmosphere" by electric discharges. (After Miller.)

The Principal Molecular Building Units

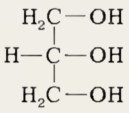
All the previously named hydrocarbons consist of carbon chains of various lengths. However, the nomenclature of acids, amino acids, etc., suggests that they must also possess specific properties characteristic only of the respective types of compounds. These properties are due to atomic groups capable of undergoing certain reactions and are therefore known as functional groups. The principal functional groups and the compounds of which they are typical are briefly discussed below.

Hydroxyl Group —OH

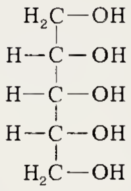
This is the functional group of the alcohols. When the group occurs singly in a molecule, the alcohol is said to be monohydric (e.g., methyl or ethyl alcohol). When the number of groups exceeds 1, the alcohol is

R—O—H	R—CH_2—OH	H_3C—OH	H_3C—CH_2—OH
Alcohol	Primary alcohol	Methyl alcohol	Ethyl alcohol

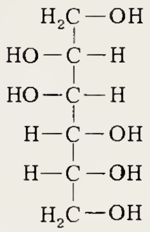
polyhydric (e.g., glycerol, adonitol, mannitol). The polyhydric alcohols with five groups are generally referred to as pentitols, and those with six groups as hexitols. The chief characteristic of the alcoholic hydroxyl



Glycerol

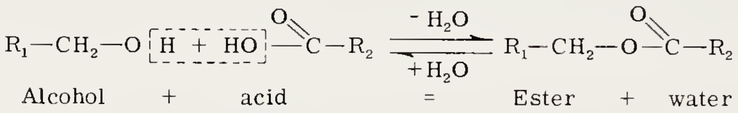


Adonitol



Mannitol

group (R_1CH_2OH) is its ability to combine with acids (R_2COOH), which themselves contain OH groups, to yield esters (R_1COOR_2), where the radical R_2 originated in the acid and R_1 from the alcohol, with simultaneous elimination of water. Experiments with isotopes have shown that



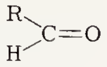
the oxygen of the water molecule eliminated on esterification comes from the carboxyl group of the acid and not from the hydroxyl group of the alcohol. An example of esterification is the formation of the biologically important glycerol phosphate by esterification of glycerol with phosphoric acid. The reverse reaction, in which an ester is split up into its components with uptake of water, is referred to as hydrolysis or saponification.

THE CARBONYL GROUP $>C=O$

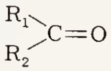
This group is characteristic of two types of compounds: the aldehydes (oxidized primary alcohols, e.g., glyceraldehyde) and the ketones (oxidized secondary alcohol, e.g., dihydroxyacetone). In metabolism they are often produced by the elimination of hydrogen (dehydrogenation) from alcohols, e.g., acetaldehyde from ethyl alcohol. The same holds for ketones; these can be derived from the aldehydes by replacing the hydrogen atom on the carbonyl group with another organic radical.

The carbonyl group is characteristic of the carbohydrates too. The basic units of carbohydrates are the sugars. These can be derived from the corresponding polyalcohols by dehydrogenation of one of the carbons. The sugars are therefore classified as pentoses, hexoses, etc.

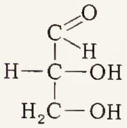
Sugars are known as aldoses (e.g., D-glucose[2]) or ketoses (e.g., D-fructose) depending on the position of the carbonyl group in the sugar molecule.



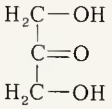
Aldehyde



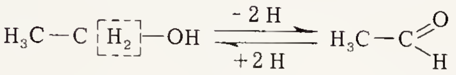
Ketone



Glycer-
aldehyde



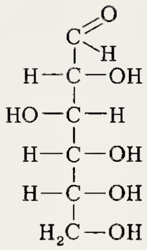
Dihydroxy-
acetone



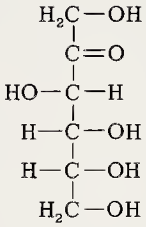
Ethyl alcohol $\rightleftharpoons$ Acetaldehyde

Sugars actually behave in many respects like aldehydes or ketones, though the open-chain formulas cannot explain all the reactions of these compounds. The Haworth ring formula is therefore often preferred. This structure must be regarded as a result of an intramolecular rearrangement (hemiacetal formation). The plane of the ring is perpendicular to the paper, with the thick lines pointing forward or upward. Depending on whether OH groups on C-1 and C-4 are on the same side or on opposite sides of the ring, the glucose is known as the α or the β form; this difference appears slight, but is nevertheless biologically extremely significant. The carbon atom (C-1) to which the carbonyl group was originally attached differs from the remaining carbons in its reactivity, and is referred to as the glucoside carbon atom.

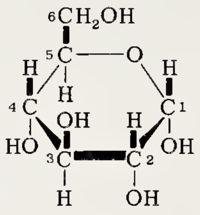
[2] Carbon atoms linked to four different atoms at the four corners of the tetrahedron are said to be asymmetrically substituted, because such carbon atom's projection of the tetrahedron yields two possible formulas which are mirror images and thus cannot be superimposed on each other (optical isomerism). The mirror forms can normally only be distinguished by their optical activity (levo- or dextrorotatory forms). According to convention, D-glucose is that form of glucose (the same also holds for other sugars) whose projected formula has the carbon atom of the highest state of oxidation at the top, and in which the OH group on the C-5 atom (counted from above) points to the right; the other isomer is known as L-glucose and the OH group in the C-5 atom points to the left. The actual direction of rotation of polarized light does not always agree with the structural formula; it must therefore be explicitly indicated, when it is significant, by the symbols + (dextrorotatory) and — (levorotatory).



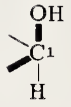
D-Glucose



D-Fructose

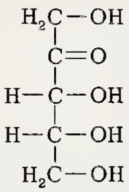


α-D-Glucose

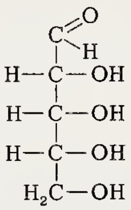


β-D-Glucose

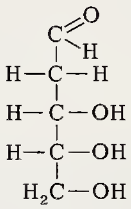
The C_5 sugars can also be divided into the aldehyde (e.g., ribose) and the keto forms (e.g., ribulose). Another biologically important C_5 sugar is deoxyribose, whose molecule differs from that of ribose in having the oxygen atom missing from C-2 (the numbering of carbon atoms starts from the top).



D-Ribulose

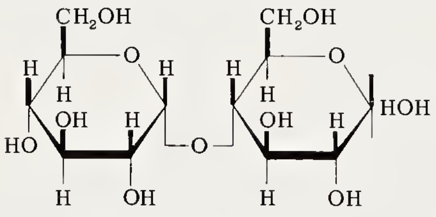


D-Ribose

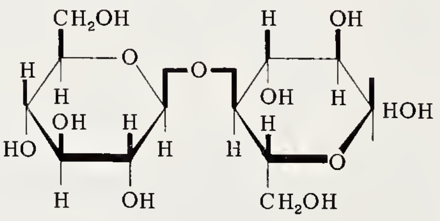


D-Deoxyribose

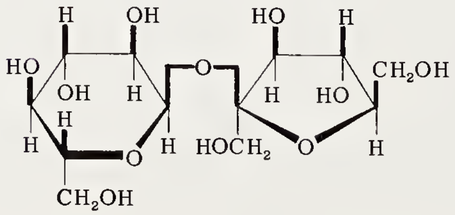
Combination of two or three sugar molecules with elimination of water (condensation) yields di- or trisaccharides. Examples of disaccharides are maltose and cellobiose. The former consists of two molecules of α-glucose, and the latter of two molecules of β-glucose. Sucrose (cane sugar) is a disaccharide consisting of one molecule of glucose and one of fructose. Raffinose is an example of a trisaccharide.



Maltose

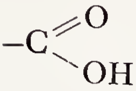


Cellobiose

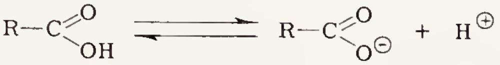


Sucrose

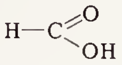
THE CARBOXYL GROUP



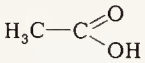
The carboxyl group, the functional group of organic acids, tends to dissociate in aqueous solution and to acquire a negative charge by losing a proton (H^+).



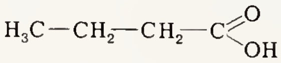
The acids are known as monocarboxylic (e.g., formic, acetic, and butyric acids), dicarboxylic (e.g., succinic acid), or tricarboxylic (e.g., citric acid), depending on the number of carboxyl groups in the molecule. The carboxyl group frequently occurs together with other functional groups in the same molecule. For example, the hydroxy acids contain both carboxyl and hydroxyl groups (e.g., lactic acid and malic acid), the keto acids carboxyl and carbonyl groups (e.g., pyruvic acid), and the amino acids (see above) amino ($-NH_2$) and carboxyl groups.



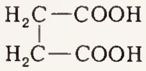
Formic acid



Acetic acid

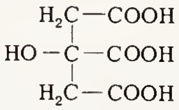


Butyric acid



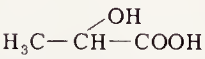
$$\begin{array}{l} H_2C-COOH \\ \quad| \\ H_2C-COOH \end{array}$$

Succinic acid

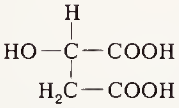


$$\begin{array}{r} H_2C-COOH \\ | \quad\quad\quad \\ HO-C-COOH \\ | \quad\quad\quad \\ H_2C-COOH \end{array}$$

Citric acid

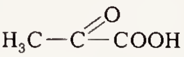


Lactic acid



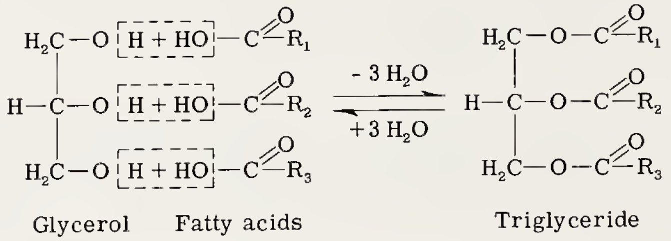
$$\begin{array}{r} H \quad\quad\quad \\ | \quad\quad\quad \\ HO-C-COOH \\ | \quad\quad\quad \\ H_2C-COOH \end{array}$$

Malic acid

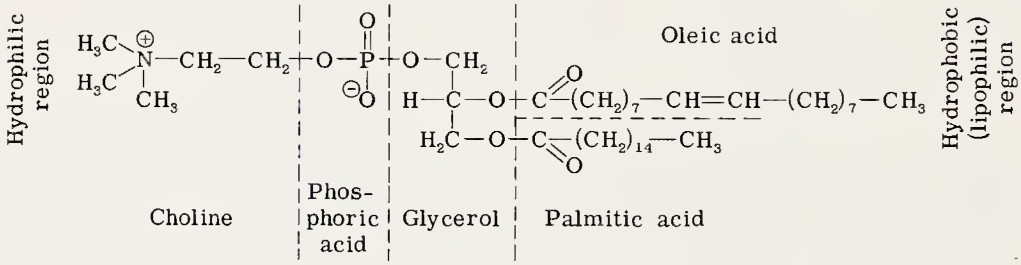


Pyruvic acid

The long-chain carboxylic acids, such as C_{16}-palmitic acid, C_{18}-stearic acid, and the unsaturated oleic acid (also C_{18} but having one double bond) are also called fatty acids since they are constituents of fats. Fats are glycerol esters (glycerides). The carboxyl group of the fatty acid provides the oxygen for the water produced in the esterification reaction (see p. 8). Fats, as esters, can be decomposed again into glycerol and fatty acids by saponification.



A group of compounds similar to the fats in certain respects are the lipids, examples of which are the phosphatides, and especially lecithin. The phosphatides are diesters of phosphoric acid. In lecithin, the acid is esterified with glycerol and with choline, an amino alcohol. Both of the free hydroxyl groups of the glycerol are esterified with long-chain fatty acids, the acid in the terminal position usually being saturated (e.g., palmitic acid) and that in the middle position unsaturated (oleic acid). The result is a molecule having both a hydrophilic and a hydrophobic (lipophilic) region.



Lecithin

The Amino Group $-NH_2$

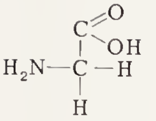
This group has a basic character, in that it acquires a positive charge by taking up a proton; it therefore functions as a cation. Although it is the characteristic group of the amines, its basic character is preserved

$$R{-}NH_2 + HCl \rightleftharpoons R{-}NH_3^{\oplus} + Cl^{\ominus}$$

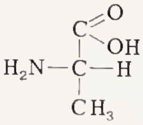
Amine

even when the nitrogen atom forms part of a heterocyclic ring, as in the pyrimidine and purine rings. These ring systems form the basis of a series of important natural products (nucleic acids): Thymine, cytosine, and uracil are based on pyrimidine rings, while adenine and guanine have purine rings.

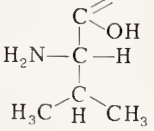
A further group of compounds carrying amino groups are the amino acids. Since these compounds also carry carboxyl groups, they exhibit



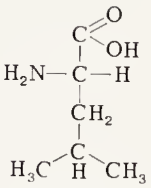
Glycine (Gly)



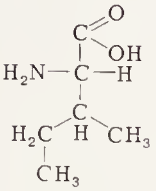
L-Alanine
(Ala)



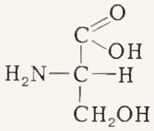
L-Valine (Val)



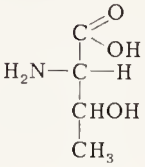
L-Leucine
(Leu)



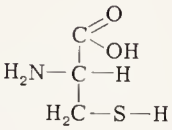
L-Isoleucine
(Ileu)



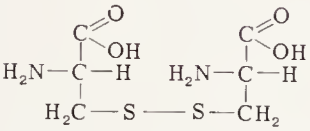
L-Serine (Ser)



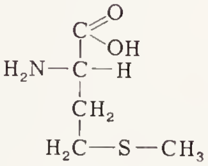
L-Threonine
(Thr)



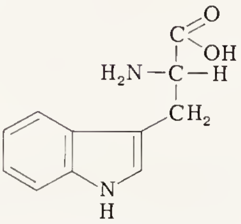
L-Cysteine
(Cys-S-H)



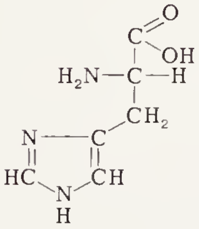
L-Cystine
(Cys-S-S-Cys)



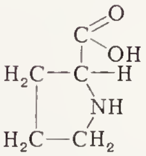
L-Methionine
(Met)



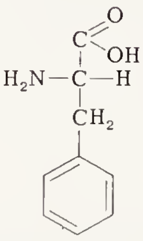
L-Tryptophan (Try)



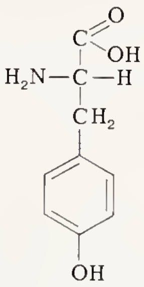
L-Histidine
(His)



L-Proline
(Pro)



L-Phenylalanine
(Phe)



D-Tyrosine
(Tyr)

both acidic and basic properties, and can therefore act as cations or as anions depending on the pH value[3] of the medium. In the absence of excess positive or negative charges the amino acid molecules are in

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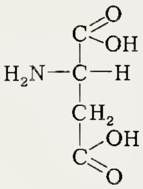
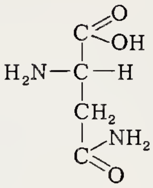
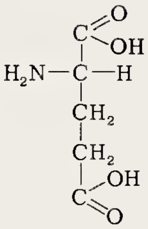
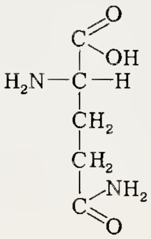
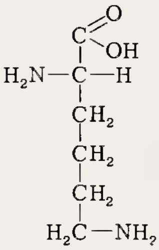
[3] The hydrogen exponent or pH value (pondus hydrogenii) is a measure of the concentration of hydrogen ions, and hence of the acidity of the solution. It is defined as the negative common logarithm of the hydrogen ion concentration: pH = — log

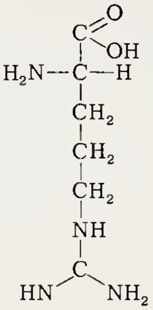

L-Aspartic acid (Asp)

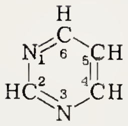

L-Asparagine (Asp-NH_2)

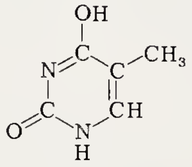

L-Glutamic acid (Glu)

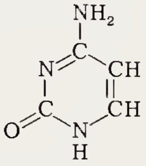

L-Glutamine (Glu-NH_2)

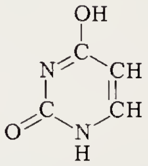

L-Lysine (Lys)

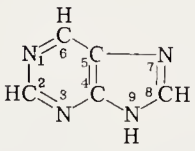

L-Arginine (Arg)

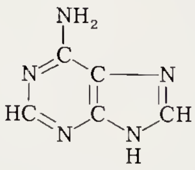

Pyrimidine

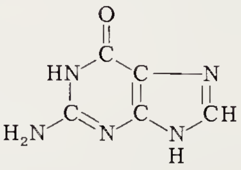

Thymine


Cytosine


Uracil

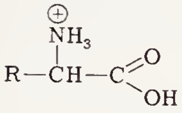

Purine

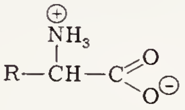

Adenine

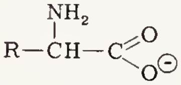

Guanine

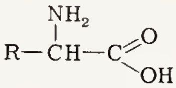
[H^+]. At room temperature, the ionic product of water is [H^+] · [OH^-] = $k = 10^{-14}$. Thus, at neutrality the concentrations of both hydrogen and hydroxyl ions are 10^{-7} ions per liter, i.e., [H^+] = [OH^-] = 10^{-7}, and the pH is 7 by definition. When the pH is numerically smaller than 7, hydrogen ions are present in excess and the solution is acidic. Conversely, the pH values of alkaline solutions are greater than 7.

the form of zwitterions (at the isoelectric point). The undissociated molecule does not exist in solution. In the amino acids that occur in proteins, the amino group is located on the carbon atom next to the carboxyl group (in the α-position). L-Amino acids are conventionally represented with the amino group on the left-hand side of the structural formula, and D-amino acids with the amino group on the right. Approximately 20 different amino acids (see pp. 13, 14) occur as characteristic components of proteins (see below). These all have the L-configuration. Other natural products, such as the mucopeptides (see p. 105), also contain D-amino acids.


Cation


Zwitterion amino acid


Anion


Undissociated molecule

Macromolecules

Although (as was shown in the previous section) a great many compounds can be built up from the relatively few elements of which plants consist, it is still difficult to explain the specificity of the numerous compounds whose occurrence is limited to certain species. Since some 300,000 plant species alone are known, each of which contains numerous species–specific substances as well as many primary and secondary metabolites of general occurrence, and since each distinctive morphological feature of an organism must have a specific material basis, it is obvious that a high degree of specificity, i.e., a great number of possible molecular combinations, is necessary.

The above requirements can only be met by macromolecules, which are built up by the repetitive use of a few relatively simple molecular units. By variation of the number of building units in a macromolecule (of which the molecular weight is a measure) and of the sequence of the building units, a practically unlimited number of combinations is possible. In this way the organisms can achieve a high degree of specificity using relatively small amounts of material and energy. This is necessary for reasons of economy in metabolism.

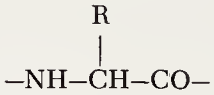
The existence of macromolecules is also a necessary condition for the formation of skeletal substances, since it is only from macromolecules that elongated fibers or reticular tissues can develop. This consideration is especially important for the structural parts of the bodies of higher plants, which are subject to high mechanical stresses.

Finally, the number of individual molecules is greatly reduced by polycondensation or polymerization, i.e., by the combination of large numbers of molecules with or without the elimination of water. Since the osmotic pressure of a solution (see pp. 35, 36) depends not on the weight of the dissolved substances but on the number of particles in solution, the formation of macromolecules allows the storage of large amounts of material in a practically osmotically inert condition.

The ability to synthesize macromolecules can therefore be regarded as essential to the life processes. Three major types of macromolecules will be discussed in the following sections: the proteins; the nucleic acids; and the polysaccharides.

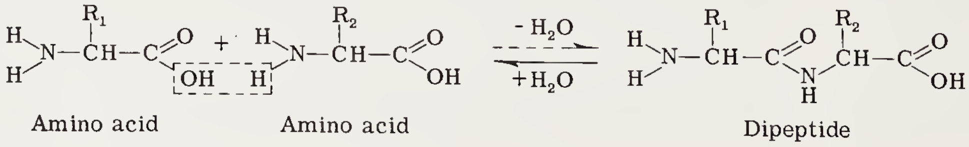
PROTEINS

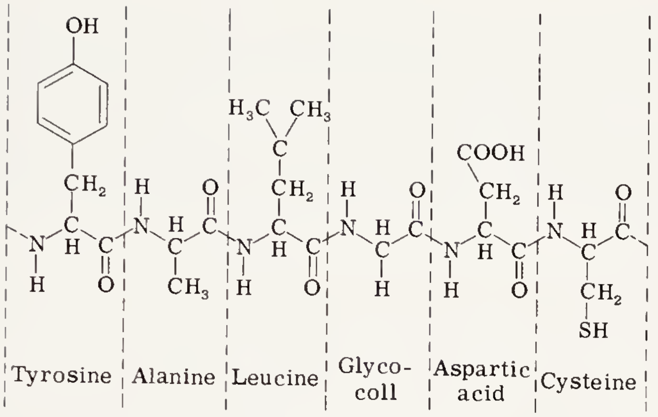
The macromolecules of proteins are built up from amino acids joined together by peptide linkages. This type of bond can be regarded as being formed by the condensation of the amino group of one amino acid with the carboxyl group of another, accompanied by the elimination of water. The equilibrium in the hydrolysis of a dipeptide is, however, shifted completely to the amino acid side, as shown by the diagram below, so that the combination of amino acids to form peptides and proteins is in fact a much more complicated process (see pp. 311–314). The amino acids are joined by the peptide linkages into chains



$$-NH-\overset{\overset{\displaystyle R}{|}}{C}H-CO-$$

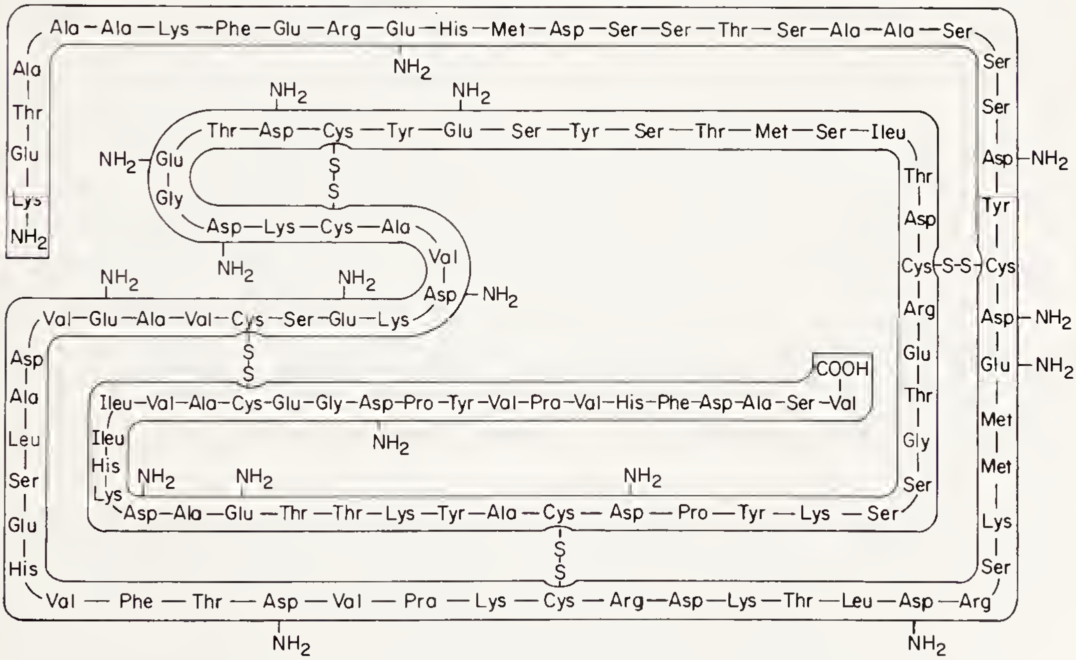
carrying the amino acid radicals R as side chains, as shown on the section of a protein molecule. If the number of components is small, the compounds are known as peptides; dipeptides consist of two, tripeptides of three, and polypeptides of many amino acid molecules. The polypeptides gradually merge into the group of proteins. The molecular weight of proteins falls in the range from 10,000 to several million.





Section of a protein molecule

As has already been mentioned, there are about 20 amino acids among the regular components of proteins. If it is assumed that each of these occurs only once in a peptide chain of 20 members, the number of possible combinations already amounts to 2.4 trillions. Since, however, protein molecules consist of several hundred or even thousand amino acid molecules, the number of possible combinations is practically unlimited. Thus, proteins satisfy very well the requirement of the highest specificity at the minimum of expense, considering that an unlimited number of compounds can be formed from only 20 components. It is therefore not surprising that every species possesses its own specific proteins.

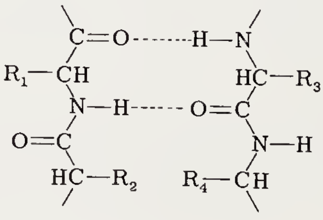

Ala–Ala–Lys–Phe–Glu–Arg–Glu–His–Met–Asp–Ser–Ser–Thr–Ser–Ala–Ala–Ser
Ser–Ser–Asp–Tyr–Cys–Asp–Glu–Met–Met–Lys–Ser–Arg
Ala–Thr–Glu–Lys–NH2
Thr–Asp–Cys–Tyr–Glu–Ser–Tyr–Ser–Thr–Met–Ser–Ileu
Glu–Gly
Asp–Lys–Cys–Ala
Val–Asp
Thr–Asp–Cys–Arg–Glu–Thr–Gly–Ser
Val–Glu–Ala–Val–Cys–Ser–Glu–Lys
Asp–Ala–Leu–Ser–Glu–His
Ileu–Val–Ala–Cys–Glu–Gly–Asp–Pro–Tyr–Val–Pro–Val–His–Phe–Asp–Ala–Ser–Val
COOH
Ileu–His–Lys
Asp–Ala–Glu–Thr–Thr–Lys–Tyr–Ala–Cys–Asp–Pro–Tyr–Lys–Ser
Val–Phe–Thr–Asp–Val–Pro–Lys–Cys–Arg–Asp–Lys–Thr–Leu–Asp–Arg
S–S
NH2

Ribonuclease

The amino acid sequence which is also referred to as the primary structure of the protein molecule, can be determined by hydrolytic cleavage and by a stepwise decomposition of the ends of the molecule. This is a very tedious procedure, but it has already been possible to elucidate the entire sequence of some molecules by this means, e.g., that of ribonuclease and that of the protein subunits of the tobacco mosaic virus (see p. 300).

In nature, proteins do not occur as straight peptide chains; the formation of hydrogen bridges between neighboring CO and NH groups of the peptide bonds (see below) produces a shape similar to a spiral (the α-helix) or to a folded sheet. This is known as the secondary structure of the proteins. Hydrogen bonds can also be formed between the hyroxyl and carboxyl groups of many amino acid chains. The steric arrangement of the peptide chains in the protein molecule is determined by the bonds between the amino acid side chains. This arrangement is known as the tertiary protein structure. As shown by the example of ribonuclease, the bonds involved are partly covalent (especially the disulfide bridges —S—S—), but ionic bonds and the so-called secondary valences (see p. 30) are also important. A protein molecule which is composed of several peptide chains is said to have a quaternary structure. This structure is homogeneous when the peptide chains are identical and heterogeneous when they are dissimilar.

Basically, a distinction can also be made between fibrous and globular protein molecules. The former are insoluble, shaped like extended fibers, act mainly as skeletal substances, and are therefore also known as scleroproteins. The shape of the globular or spheroproteins is compact, approximately spherical. This group can be subdivided into the albumins, which are water soluble, and the globulins which are insoluble in pure water but soluble in salt solutions. Finally, a distinction must be drawn between simple and conjugated proteins: The former are composed only of amino acids, while the latter contain, apart from a protein component, some other, nonprotein parts (prosthetic groups). Some plant pigments, for instance, occur as chromoproteins, i.e., the pigment component constitutes the prosthetic group. Other examples are the nucleoproteins, lipoproteins, and enzymes.



Hydrogen bonds

Proteins are built up from amino acids, which accounts for their many common properties. Proteins, too, exhibit an isoelectric point, at which the numbers of positive and negative charges on the molecule are equal. At this point they are relatively unstable and tend to flocculate from solution. In acid media proteins are split up or hydrolyzed; this process is accompanied by the uptake of as many water molecules as were eliminated on peptide formation.

NUCLEIC ACIDS

The nucleic acids differ from proteins mainly in that the molecular components of the former do not belong to a single class of compounds. The molecular chains of nucleic acids are built up from nucleotides, which consist of three components: phosphoric acid; sugars (pentose); and bases (purines and pyrimidines). These combine with each other in the sequence: phosphoric acid–pentose–phosphoric acid–pentose, as shown by Fig. 1.7, the bases forming side branches on the sugar molecules. There are fundamentally two types of nucleic acids which differ with respect to both their sugar components and the base composition. Deoxyribonucleic acid (DNA), which was formerly also called thymonucleic acid, contains D-deoxyribose as the sugar and the bases thymine, cytosine, adenine, and guanine. Ribonucleic acid (RNA), on the other hand, contains D-ribose as the sugar and the bases uracil, cytosine, guanine, and adenine. In RNA, thymine is thus replaced by uracil. A few other bases, which have so far only been found occasionally, have been omitted here. The combinations of bases and sugars are referred to as nucleosides; corresponding to the base they are known as adenosine, cytidine, guanosine, thymidine, and uridine. The combinations of nucleosides with one, two, or three phosphate groups are known as nucleotides; thus, in the case of adenine one can distinguish between adenosine mono-, di-, and triphosphate (see pp. 195, 196).

Quantitative analysis of DNA has shown that the numbers of molecules of purine and pyrimidine bases in DNA are equal, and that the thymine: adenine and the cytosine:guanine mole ratios are also equal to 1. The thymine:cytosine (or, what amounts to the same thing, the adenine: guanine) mole ratio, however, is subject to wide variations in different organisms. This indicates the existence of specific pairing between thymine and adenine and between cytosine and guanine. It was on this basis that Watson and Crick[4] developed their structural model of DNA

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[4] Watson and Crick received the 1962 Nobel prize for medicine for this work, together with M.H.F. Wilkins who confirmed the model experimentally.

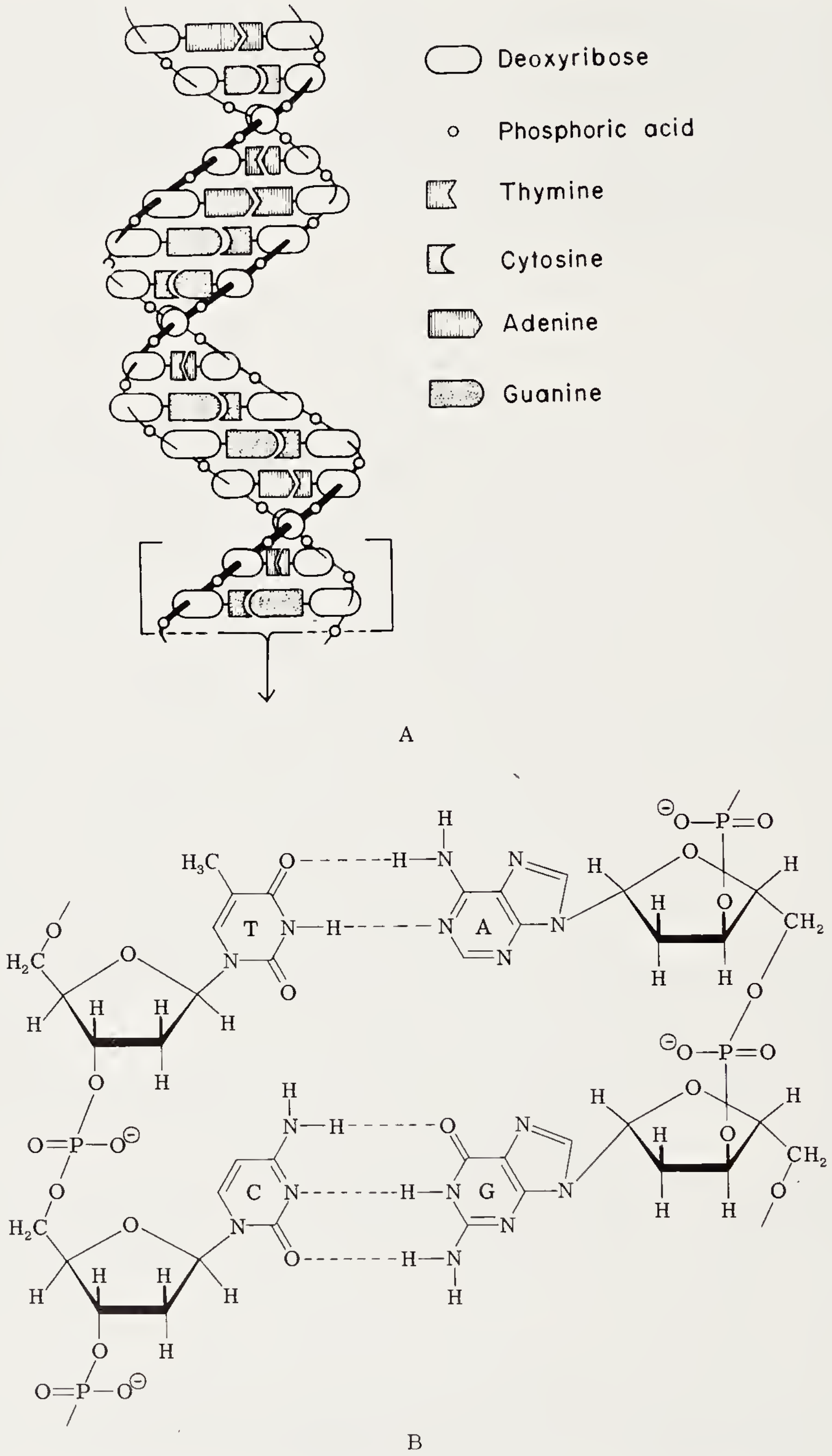


FIG. 1.7. Watson-Crick model of deoxyribonucleic acid (DNA). (A) Structure of the double helix; (B) specific pairing of bases.

reproduced in Fig. 1.7. According to the Watson-Crick model, the structural unit of DNA consists not of one but of two parallel, unbranched, polynucleotide chains, wound around a common axis in a right-handed helix. A single turn comprises about 10 nucleotide units in each chain. The phosphate groups are located on the outside and are easily accessible to cations. The bases are perpendicular to the axis and point inward; thymine is located opposite adenine any cytosine opposite guanine. Figure 1.7B shows that hydrogen bonds are formed between the neighboring amino and keto groups of the respective bases, which make any other type of base pairing sterically impossible. The two chains are therefore not identical but complementary.

As has already been indicated, DNA occurs in the cell as a nucleoprotein. It is assumed that histones, a group of basic proteins which occur together with nucleic acids, are tightly bound to the DNA helix, or may even occur as a third strand of a wider coil. No details are as yet available at this point. The Watson-Crick model has so far been able to explain all problems that have arisen, and it can therefore be regarded as well substantiated.

In spite of the fact that there are only four types of nucleotide building units, the DNA molecules are highly specific. The reason for this specificity is that more than 100,000 nucleotide units can combine in one chain, as shown by the high molecular weights which can run to eight million. The variability is again due to variations in the nucleotide sequence; this sequence is apparently not periodic. Moreover, DNA is capable of self-replication (see p. 297) and, as such, is suitable as a genetic material.

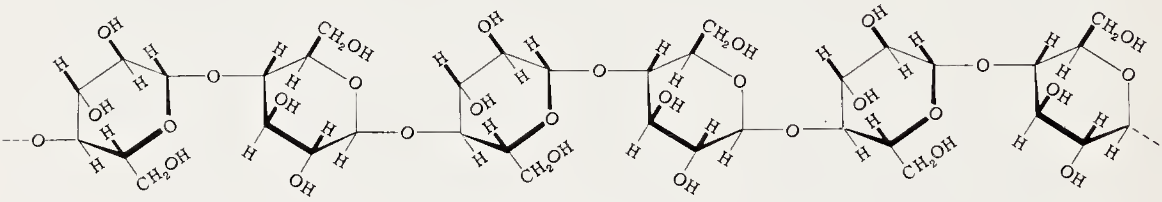
In ribonucleic acid, the nucleotides are similarly paired in chains but it is not known whether or not they possess the same secondary structure as DNA. RNA occurs mainly as a single molecular chain, though double strands also seem to occur. Basically, there are two RNA fractions distinguished by the order of magnitude of their molecular weights. The soluble material, also known as sRNA or transfer-RNA, has a molecular weight in the range of 20,000–40,000, while the structural RNA has molecular weights in the region of 500,000–2,000,000. The function of the two fractions appears to be completely different (see p. 312).

POLYSACCHARIDES

The macromolecules of the polysaccharides belong to the group of carbohydrates, and in contrast with the proteins and nucleic acids are mostly built from a single type of molecule. Various sugars can act as the structural units; the sugar molecules combine with simultaneous elimination of water (polycondensation). The C-1 and C-4 atoms of neighboring rings are linked together most frequently but other types of bonding also occur. The possibilities for variation therefore consist of the use of various sugar molecules as the basic units (though each macromolecule is built of only one type of sugar), the way in which the individual members are linked, and the chain length; these are rather limited in number compared with the proteins and nucleic acids. Polysaccharides are therefore not species-specific materials but fulfill other functions.

CELLULOSE

The significance of cellulose for plants is due to its suitability as a skeletal material (see pp. 65–67). Cellulose is built up from glucose molecules linked by β-glucoside links. The macromolecules so produced have a zigzag arrangement, with the segments at angles of 107°, of extended threadlike shape, each thread containing up to 8000 glucose molecules. The basic unit is the disaccharide cellobiose (see p. 10).



Cellulose

STARCH

The starch molecule is also built up from glucose, but the glucose molecules are linked by α-glucoside links. The basic structural unit is therefore maltose, and the macromolecule is not extended but wound in the shape of a regular coil, each turn consisting, as shown in the diagram, of six glucose molecules. The amylose molecule consists of about 300 glucose molecules and has the shape of an unbranched coil (Fig. 1.8A). Amylopectin, too, occurs in native starch; this molecule can be built from up to 1000 glucose units, and exhibits multiple branching (Fig. 1.8B). The individual branches consist on average of about 25 glucose molecules, and are also wound into coils.

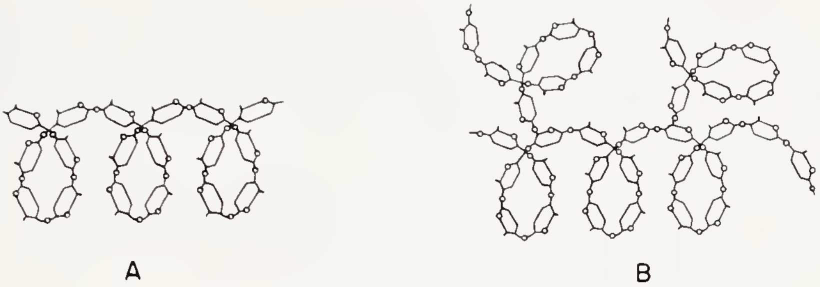
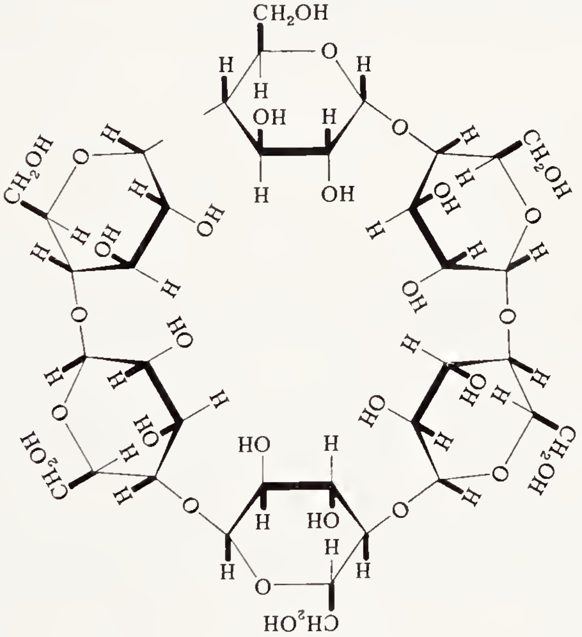


Fig. 1.8. Schematic arrangement of the glucose molecules in starch.

The normal links in both amylose and amylopectin are 1,4, i.e., the C-1 atom of one ring is linked to the C-4 atom of another. Consequently, the starch molecule terminates at one end in a glucoside C-1 atom and at the other end in a C-4 atom. Therefore, one can distinguish a reducing and a nonreducing end (see p. 226). The branching of the amylopectins occurs through 1,6 linkages.



Starch

In view of its structure, starch is not a suitable skeletal material. However, it enables the living plant to convert glucose, a very useful energy source, without major alteration of the molecule, into an insoluble and therefore osmotically inert form from which it can again be mobilized at any time. Starch is therefore the most widespread reserve material in plants (see pp. 77–78). Other polysaccharides that serve as the reserve materials for certain plants include glycogen, which also consists of glucose units and is still more branched than amylopectin, laminarin, leucosin (=chrysolaminarin, see p. 111), and paramylon (see p. 51), all of which occur in algae and whose glucose units are joined by 1,3 links and also insulin, which is built up from fructose molecules (see p. 78). The molecules of callose, whose function will be discussed later (see p. 87), also consists of glucose chains with 1,3 links.

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Chapter 2

The Structural Constitution of Protoplasm

While organisms do indeed consist of molecular building units, they are far from being random accumulations of molecules. The proteins, nucleic acids, lipids, and other components of the organism exist in highly ordered structures whose details have by no means yet been fully clarified. These structures are very labile and can only be maintained against the entropy gradient[1] by a constant supply of "free energy" (see p. 195). This state of affairs has aptly been compared with that of a leaking ship which can remain afloat only by making constant use of its pumps. If the energy supply is cut off, the state of order collapses.

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[1] Entropy is a measure of the ordering of matter at the molecular level, or, stated differently, it is a measure of the distribution of energy. Disordered states are more probable than ordered ones. The transition into a disordered state is described as an increase in entropy, and the realization of an ordered state as an entropy loss. According to the second law of thermodynamics, spontaneous processes are always accompanied by a net gain in entropy. The development of a more highly ordered state, or the production of a thermodynamic potential is therefore only possible when this entropy loss is compensated for elsewhere by a corresponding gain in entropy.

The state of order manifests itself in the development of certain molecular arrangements. These can sometimes be observed through the optical (or, more usually, electron) microscope, and are known as structures. Structures should be regarded as a higher development of molecular aggregates; they are characteristic of the substrate of the active vital processes which is known as the *protoplasm.*

Biochemical reactions can also occur outside the living organism, as long as the reacting substances are in solution. The situation becomes more complicated in the so-called chain reactions, in which the end product of one step serves as the starting material for the next. If a chain reaction passes through a great number of intermediate steps, as does the respiration reaction (see pp. 229–231), then it can hardly proceed in a controlled manner in the absence of a definite steric arrangement of the reacting substances. In a free solution the reaction depends on chance collisions of the reacting molecules, and its probability will in consequence decrease with increasing dilution.

From the chemical point of view the structures in the protoplasm are not homogeneous but consist of several components. These can act partly as active components essential to the reaction and partly as mere structural supports determining the form of the components. The protoplasmic structures invariably have specific tasks, i.e., carry out various but quite distinct functions, and this variety of function is reflected in their morphological features.

Lamellae are systems of thin sheets or "membranes" either extracellular or penetrating the ground substance and acting apparently as carriers of certain active chemical groups. Their function is undoubtedly the provision of the maximum surface area for chemical reactions. Examples of extracellular laminae might be the basement lamina (mucopolysaccharide layer) of animal epithelia or the "middle lamella," of plant cells.

Membranes are lamellae, usually a double membrane (see below), around cell organelles such as plastids or mitochondria, or bounding the cell (plasma membrane), or vacuole (tonoplast), or as living extensions of the cell (plasmodesmata through pit areas). The most widely accepted concept of the nature of each lamella of the membrane is a trilamellar structure ("unit membrane," Robertson) consisting of a protein layer on each side of a lipid layer. The function of the membranes is to subdivide protoplasm into reaction compartments (principle of compartmentalization).

Fibrous and reticular structures penetrate the protoplasmic ground substance as single threads or as a skeletal framework, e.g., filaments, microbodies, and particularly the endoplasmic reticulum. The same holds true for tubular structures, the microtubules, which may also be joined into networks. The endoplasmic reticulum and the nuclear membrane may join to form a continuous network (see p. 56).

The ordering of molecules, especially that of macromolecules into structures, has no doubt been a decisive step in the development of organisms. The question of how this step could have occurred is still a subject for hypotheses, whose merits and demerits cannot be argued here. At any rate, it is clear that it could only have occurred by the absorption of energy. If, as explained in the previous chapter, the possibility for protein and nucleic acid synthesis is assumed at a certain phase of the development of the earth (in the primeval sea) then these macromolecules must have been stabilized immediately after their formation; otherwise, they would have disintegrated again. The possible mechanisms for stabilization are, e.g., adsorption on certain minerals, perhaps on clays, or the formation of coacervates—droplike mixtures of organic substances in dilute colloidal systems. According to Oparin, such coacervates could accumulate more organic compounds from the environment and finally divide into parts similar to the original coacervates and behave in the same way. As the coacervates had to be maintained in steady interaction with the environment, we can, with some justification, regard this era of evolution as having seen the origin of structures that could, for instance, have developed at the surfaces of coacervates to control the intake of materials. In this manner primitive material systems could have developed, having the ability to exist and to reproduce by utilizing the organic materials available in the primeval sea. There is as yet no experimental support for these hypotheses.

The Basic Structure of the Protoplasm

To summarize, the protoplasm can be described as an organized mixture of many organic and inorganic materials existing in the aqueous phase, partly in solution and partly in colloidal dispersion. The bulk of its mass consists of water, and normally accounts for 60–90% of the material, or exceptionally in certain aquatic plants and animals for as much as 98%. The dry matter obtained on removal of the water consists mostly of about 68% proteins, 15% lipids, and 14% carbohydrates. The rest is made up of nucleic acids, inorganic salts, and many other compounds, whose proportions vary from case to case (Lepeschkin, 1923).

Owing to their high molecular weights and the concomitant molecular size[2] the proteins in the aqueous phase (amino acids) mostly belong to the colloids; the colloidal size range, as defined by Ostwald, falls between 1 and 100 nm (1 nm = nanometer = $m\mu$ which is equal to 10 Å or 10^{-6} mm). Proteins and colloids have many properties in common, but it must be remembered that the colloidal particles are aggregates of smaller units, while proteins, as a rule, exist in solution as single (even though large) molecules which cannot be further subdivided without altering their specific properties.

Protein molecules may be either *globular* or *fibrous* in shape, or both, depending upon the salt concentration in the cell. Ultimately proteins may be characterized on amino acid content and linkages between these mixed acids, but presently they are distinguished from one another primarily on the basis of their solubility. For example, *albumin, histone,* and *protamine* are neutral water soluble; *globulins* are soluble only in dilute neutral salt solutions; *prolamines* (e.g., gliadin of wheat) are soluble only in alcohol solutions, some are soluble only in acid or basic solutions (*glutelins* of cereals); and *scleroproteins* or *albuminoids* are essentially insoluble.

A protein solution of simple molecules therefore corresponds to a sol from the colloid chemical point of view. Similar to colloids, proteins can undergo gelation when present in sufficient concentration. Gelation involves cross-linking and the formation of a loose protein molecule network, the pores of which are filled with water (Fig. 2.1). This is basically just as possible for fibrous (Fig. 2.1A) as for globular proteins (Fig. 2.1B), but the tendency toward gelation is naturally higher in elongated fibrous macromolecules. The gel solutions in which the molecules are partially cross-linked but do not yet form a coherent network are intermediate between the sol and gel state.

The protein molecules can be joined by primary and secondary valencies, i.e., in principle by the same types of bonds that account for the secondary, tertiary, and quaternary structures of proteins (see p. 18). In addition to the hydrogen bonds between the CO and NH groups of the peptide bonds, the side chains of protein molecules, i.e., the amino acid radicals with their functional groups, also take part in the bridging. Depending on whether the groups are polar (hydrophilic: carboxyl, hydroxyl, carbonyl, amino groups), or apolar (hydrophobic: methyl, ethyl, phenyl radicals), the following types of bonds can be distinguished (Fig. 2.2).

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[2] The size of a molecule depends not only on its molecular weight but also on shape. There is, therefore, no strict parallel relationship.

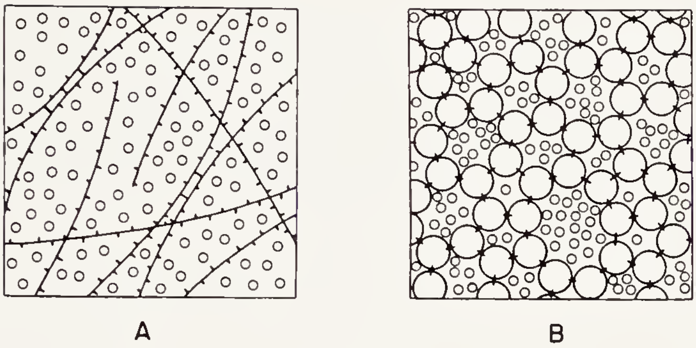

FIG. 2.1. Cross-linking of (A) fibrous and (B) globular proteins. The small spheres represent water molecules. (After Frey-Wyssling, modified.)

COVALENT BONDS (see p. 3)

Examples are the very common disulfide bridge–S–S– and the rarer ether bond –O–, produced with the elimination of hydrogen –S–$\boxed{\text{H H}}$–S and water –O–$\boxed{\text{H H}}$–O–, respectively. These are primary valencies and as such are very strong. Under physiological conditions they can only be broken in reactions involving enzymes (see pp. 197–198).

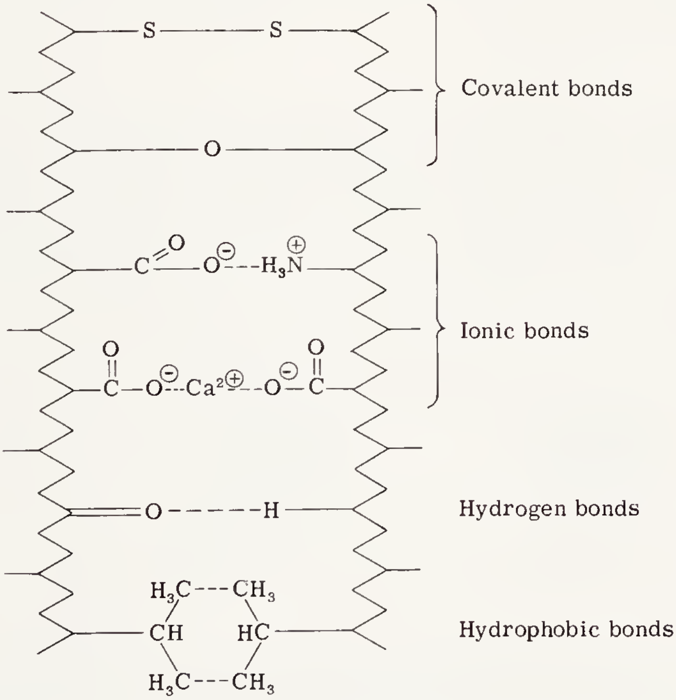

FIG. 2.2. Possible bonds between protein molecules.

IONIC BONDS (see p. 3)

Molecules are generally bridged by divalent ions, such as those of calcium or magnesium, which can bind two singly charged carboxyl groups. Although these bonds too are relatively strong, they can be broken under physiological conditions by hydrolysis and are therefore pH-dependent. The bond between an NH_3 and a carboxyl group is also ionic in character (Fig. 2.2), but it is weaker and is rather like a secondary valence.

HYDROGEN BONDS AND DIPOLES

Hydrogen bonds, whose significance for the secondary structure of proteins has already been indicated (see p. 18), are important in the formation of protoplasmic structures. These bonds are classified among the secondary valencies, and according to recent studies, their magnitude amounts to only one-fiftieth of that of a primary bond. Valence forces can also arise out of interactions between dipoles and ionic or other charges. Thus, the hydration shells which develop in the electric fields of charged groups (Fig. 2.3) can also contribute to bonding.

HYDROPHOBIC BONDS

Such bonds are produced when apolar groups of amino acid side chains come into contact and are thereby to a certain extent withdrawn from the aqueous phase. Hydrophobic bonds originate from van der Waal's forces between apolar groups, and are strongly affected by the surrounding medium. In view of their secondary valence character, they are relatively weak. For example, they can be easily broken by small increases in temperature; this is one of the reasons for the decreasing viscosity of protoplasm with rising temperature.

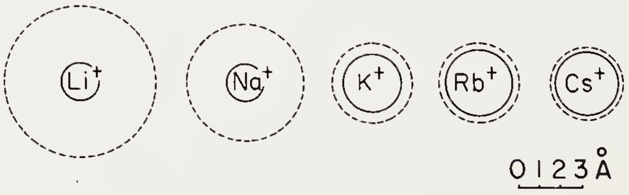

FIG. 2.3. Shells of hydration of the alkali metal ions (broken lines). [After Frey-Wyssling (1948).]

It follows from the diverse character of the bonds that the degree of cross-linking, thereby also the state of swelling of the protoplasm, can be affected to various degrees by changes in the external conditions. Swelling is a reversible increase in volume caused by the penetration of solvent molecules between the molecules of the body capable of swelling; in the present case, it is the penetration of water between protein molecules.

Water molecules in themselves are known to be neutral, but as a result of the bond angle of the oxygen atom, the charge distribution in the molecule is not symmetric; the positive charges predominate on one side and the negative charges on the other (Fig. 2.4A). The water molecule is therefore a dipole. In consequence, particles carrying an electric charge attract water molecules and surround themselves with a shell of hydration in which either the positive or the negative poles of the water molecules face the particles, depending on the particle charge (Fig. 2.4B). Electrically neutral particles can also develop a shell of hydration if their charge distribution is nonhomogeneous (Fig. 2.4C).

The size of a shell of hydration depends partly on the number of charges and partly on the size of the particles. This is clearly demonstrated by the series of alkali metal ions on which the charge is constant. The charge density at the surface, and so also the thickness of the shell of hydration, decreases with increasing ionic diameter (Fig. 2.3). The position is similar for other hydrated particles, e.g., the plasma proteins.

Every alteration in the charge, possibly due to changes in pH, must therefore necessarily affect the thickness of the shells of hydration and so the degree of swelling. The degree of swelling is also affected by the addition of ions. If present at low concentrations, they tend to cause shrinking. This shrinking becomes more pronounced as the shell of

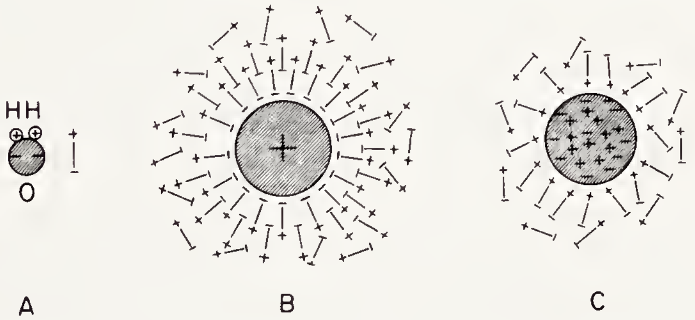

FIG. 2.4. Hydration: (A) the water molecule as a dipole; (B) hydration shell of a particle with excess positive charges; (C) hydrated isoelectric particle with a symmetrical charge distribution. [After Pallmann (1931), modified.]

hydration becomes smaller, i.e., the nearer the ion can get to the proteins and neutralize their charges. Thus, in the case of alkali metal ions the deswelling ability increases from Li^+ to Cs^+.

The ion antagonism between K^+ and Ca^{2+} is especially important for plants. Owing to its bivalence, Ca^{2+} shields the charges of plasma proteins and reduces swelling more effectively than does K^+.

The condition of the protoplasm is therefore subject to strong variations, so that it sometimes appears fluid and sometimes gel-like. Continuous sol–gel transformations also occur as networks of protein molecules build up and break down. From the chemical point of view, too, the concept of the network is not static but dynamic, as individual sections of the network are constantly rebuilt and renewed (see p. 242).

The generally labile nature of the protoplasm and its susceptibility to chemical and physical effects results in *denaturation,* if the attack is severe. This is a process of irreversible shrinkage and other alterations in the structure which lead to loss of biological activity and finally to death of the protoplasm. Denaturation is often accompanied by *coagulation,* i.e., precipitation. This effect can be observed for instance when plasma is treated with several plasma poisons also used as fixing materials in microscopy (alcohol and formaldehyde). The bonds are partly destroyed in the process. Denaturation involves a transition into a state of lower order and is therefore accompanied by a gain in entropy.

The Lamellar Structural Principle

Electron microscopic studies of recent years have shown that optically homogeneous protoplasm is in reality penetrated by numerous structures; the basic unit of these structures is usually the elementary or *unit membrane.* At high resolution it appears as a dark double line enclosing a lighter inner space [see plasmalemma (pm) in Fig. 3.6E]. The thickness of the unit membranes amounts to 70–100 Å, depending on the object and on the method of preparation. Double membranes are frequently found (see p. 26) which consist of two unit membranes (Fig. 2.5).

The "unit membrane" terminology reflects the apparent similarity of these membranes in electron micrographs, and is therefore a micromorphological concept. The views concerning the molecular structure of these membranes still differ at present. What is known for certain is that the membranes consist essentially of proteins and lipids. The structure reproduced in Fig. 2.6A has been proposed by Danielli. According

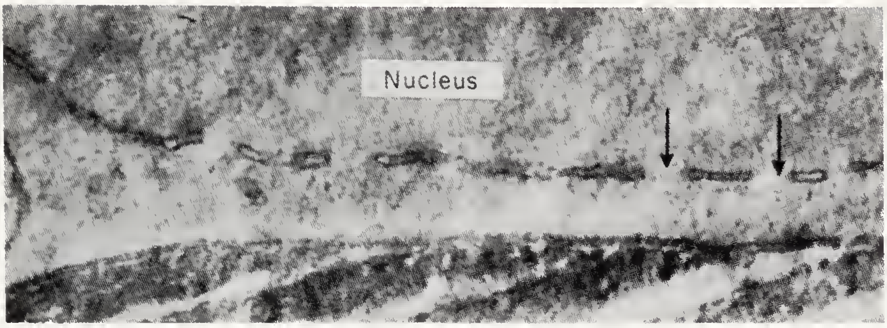

FIG. 2.5. *Euglena gracilis.* Electron micrograph of an ultrathin section through the nuclear membrane as an example of a double membrane. The resolution of this micrograph is fairly low, so that the three-layered structure of the unit membranes is not discernible. Some pores are indicated by arrows. The double membrane surrounding the chloroplasts is well resolved at lower left. Fixed in $KMnO_4$, magnification approx. 65000×. (Original photograph by Dr. W. Könitz.)

to this model, the membrane's consist of a bimolecular lipid film in which the lypohilic regions surrounded by shells of hydration are turned outward (cf. p. 261). The film is covered on both sides with a layer of similarly hydrated protein molecules. Occasionally, however, the reverse arrangement seems to occur too (Fig. 2.6B). According to other authors the membranes consist of alternating protein and lipid units arranged so that the hydrophilic regions point outward and the lipophilic region inward.

The function of the membranes also varies considerably in spite of their uniform appearance in the electron microscope. This is apparent already from the very different biochemical performance of the individual cell organelles (see below). It must therefore be assumed that the membranes contain further molecular units, e.g., enzymes, which

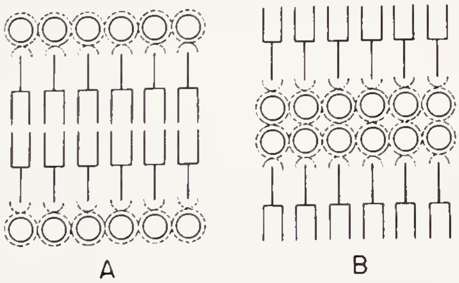

FIG. 2.6. Model of a lipoprotein membrane (unit membrane). The prongs of the forks represent the lipophilic and the handles the hydrophilic regions of the lipid molecules, the latter with shell of hydration. The protein molecules are shown as circles and are also hydrated. (A) and (B) show two possible types of membrane.

perform distinct functions in determining the specificity of the biochemical performance of the membrane.

The composition and structure of the membranes explain their properties: on the other hand, their ability for rapidly extending their area by inclusion of new units (intussusception); and on the other hand, their selectivity, enabling them to allow rapid passage of certain materials while retarding the passage of others. In extreme cases this leads to semipermeability, i.e., to a strongly reduced permeability for the solute but good permeability for the solvent. In this context it is necessary to discuss the physical processes occurring at *semipermeable* or *selective* membranes; these membranes control the movement of materials by pore size, electrical charge, or concentration difference.

The tendency of a gaseous or dissolved substance to fill homogeneously the space available to it, i.e., to distribute itself evenly throughout the volume of the fluid, is known as *diffusion.* Diffusion is caused by thermal kinetic energy of molecules, which can be demonstrated by the so-called Brownian movement. As a result of constant impacts of solvent molecules, any small suspended particles, such as droplets of an emulsion if their diameter is smaller than 5 μ, are set into jerky irregular motion. This phenomenon was first observed by Robert Brown (1827), and it can easily be seen under a microscope in a drop of milk or in a water suspension of India ink (Fig. 2.7).

If a crystal of a dye or a colored salt is placed in an upright cylinder filled with water, the solution will at first become strongly colored at the bottom of the vessel. If the cylinder is allowed to stand undisturbed, the dye will distribute itself uniformly throughout the cylinder in the course of a longer period of time, even upward against the force of gravity. Diffusion is characterized by the relationship $s_x = s\sqrt{x}$, where x is the number of days and s is the distance covered in a day. Over short distances the motion is therefore fairly rapid, while longer periods are necessary to cover greater distances. The rate of diffusion is in-

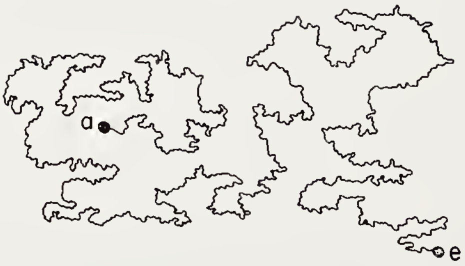

FIG. 2.7. Path of a particle exhibiting Brownian movement: (a) start; (e) end of path. (After Pekarek, modified.)

versely proportional to the molecular weight (M): $D = \text{const.}/\sqrt{M}$ where D = diffusion coefficient

If two solutions of unequal concentrations (one of which could be pure water) are separated by a selective membrane, the tendency of the dissolved molecules and ions for diffusion will be affected by pore size relative to molecular size in the case of molecules and by the charge on the membrane in the case of ions. The resulting diffusion potential forces *water* across the membrane into the solution of higher concentration. This process is called *osmosis.* The steady uptake of water by the osmotically active system causes an increase in volume and thereby an expansive pressure: the osmotic pressure.

If, for instance, a crystal of potassium ferrocyanide is placed in a solution of copper sulfate, a selective membrane of copper ferrocyanide is precipitated on its surface after only a short time.

$$K_4[Fe(CN)_6] + 2\,CuSO_4 \rightarrow Cu_2[Fe(CN)_6] + 2\,K_2SO_4$$

As further molecules of the potassium cyanide crystals continue to pass into solution, the concentration and also the osmotic pressure of the solution increases in the volume enclosed by the membrane until the membrane bursts. The two solutions then come into contact again and a new membrane is formed immediately. Bizarre structures arise in this way which continue to grow until the whole crystal has dissolved. This system has also been described as a Traube cell.

Osmotic pressure can be measured by means of an osmometer, which in the simplest case consists of a glass belljar fitted with a standpipe and closed at the bottom by a selective membrane, e.g., a collodion sheet. After the experimental solution has been added, the lower part of the belljar is immersed in a solution of lower concentration. The water column rises in the standpipe until the hydrostatic pressure of the column is equal to the osmotic pressure. The value measured in this way is known as the osmotic pressure of the solution and is expressed in atmospheres.

Since the membranes described above are not strictly selective, Pfeffer developed a system, now named after him, in which the selective membrane is produced by precipitation of copper ferrocyanide in the capillaries of a clay cylinder. The Pfeffer cell is filled with the test solution and the pressure produced is read on a mercury manometer (Fig. 2.8). Measurements of this kind have revealed certain regularities which are summed up in van't Hoff's theory of solutions: (1) At constant temperature, the osmotic pressure is proportional to the concentration; (2)

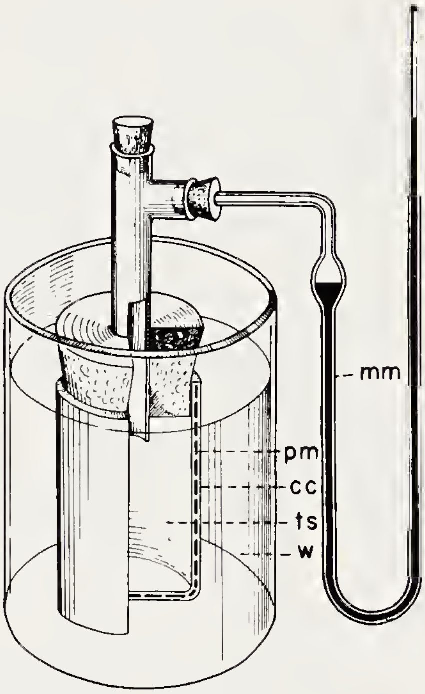

FIG. 2.8. Pfeffer's cell. Quarter sections of the front of the clay cylinder and of the tube at the top have been cut away. cc, Clay cylinder; mm, mercury manometer; pm, precipitated membrane; ts, test solution; w, water.

at constant concentration, the osmotic pressure is proportional to the absolute temperature; (3) equimolar solutions, i.e., solutions containing equal numbers of particles, are isoosmotic (isotonic). Salts constitute an exception, being always partly dissociated into ions, so that the number of particles is greater than the number of molecules. For example, the osmotic pressure of a molar potassium nitrate solution is 1.69 times that of an equimolar solution of cane sugar. The value of 1.69 is known as the isoosmotic coefficient.

The selective characteristics of the lipoprotein membranes make them eminently suitable for functioning as physiological barriers in living organisms, insofar as they separate individual reaction compartments and prevent uncontrolled mixing of dissolved substances. Their selectivity is in any case not absolute; rather, they can be regarded as being permeable to solutes to a certain extent over longer periods of time. The permeability depends on the size of the solute molecules first; the membrane, which acts as an ultrafilter, will allow the passage of smaller molecules rather than of larger ones. The lipid solubility is the second factor affecting the passage of a substance through a membrane containing lipids. Finally, the electric charges carried by the particles also play a part, since it has been confirmed in at least some cases that the membranes themselves are charged. Thus, for instance, the plasma boundary layers of the cell are permeable to K^+ ions but hardly permeable to Ca^{2+} and Na^+ (selective ionic permeability, see p. 378).

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Chapter 3

The Cell

The term "cell" was introduced by Robert Hooke, who discovered the cellular structure of cork in 1667. Although evidence for the general cellular structure of plants was put forward soon afterwards by Marcello Malpighi in his "Anatome Plantarum" (1675–1679), the significance of protoplasts was recognized only much later. The term *protoplast,* proposed by Hanstein in 1880, denotes the protoplasmic contents of a cell. According to older usage the extranuclear portion of the protoplast was called *protoplasm,* which was unfortunate since the *nucleus,* the controlling center of the cell, is also composed of protoplasm, or living substance in its broadest sense. We now use Strasburger's term *cytoplasm* to describe the protoplasm within the cell and *nucleoplasm (karyoplasm,* Flemming) for the protoplasm in the nucleus. The observation of cell division by Dumortier and Meyen at the beginning of the nineteenth eentury and the discovery of the nucleus by Robert Brown (1831) was followed in 1838–1839 by the cell theory of Schleiden and Schwann. Wirchow formulated his basic "omnis cellula e cellula" principle in 1855; this year is regarded, with some justification, as the date of birth of classic cytology. Cytological research reached a peak in 1875 with the discovery of nuclear division in plants and animals by Strasburger, Bütschli, and Flemming. Advances in cytology have ever since been closely connected with the development of microscopic techniques. Important progress has been brought about first by the introduction of phase contrast and then the polarizing microscope and fluorescence microscopy in the first half of this century; we owe our present knowledge on the structure of the cell to the development of the electron microscope.

While it is true that the protoplasm is the substrate of life processes, this does not mean that any arbitrarily small part of the protoplasts can be regarded as "alive." Although the protoplasm and its structural elements can under certain conditions fulfill some biochemical functions outside the organism, the ability to control and coordinate these functions is bound up with the cellular level of organization. As shown by the numerous microbes, the cell is the smallest morphological unit capable of independent existence and exhibiting all the attributes of life. If the cell is destroyed, or if the basic cell organelles are removed, it also loses its ability to live. *Organelles* are submicroscopic inclusions in the cytoplasm, with a characteristic structure and function, e.g., plastids, mitochondria, ribosomes.

Plant cells vary tremendously both in size and in shape. The size can vary between the extremes of about 1 μ (for certain bacteria) and a half meter [fibrous cells of ramie *(Boehmeria nivea)*]. The average diameter of nonfibrous cells lies approximately in the range of 20–200 μ. The shapes of cells often depend on their function. This will be discussed later (see p. 89).

The Cytoplasm

The protoplast in a typical plant cell is surrounded by a cell wall. The bulk of the mass of the protoplast consists of *cytoplasm.* This encloses the nucleus and contains many other enclosures which either have specific functions, like mitochondria and plastids, or are metabolites such as fat droplets and starch grains.

The cytoplasm fills the embryonic cell completely (Fig. 3.1A,B). It appears quite homogeneous in the optical microscope, or more seldom granular, and contains, apart from the relatively stable and self-contained enclosures like the nucleus and plastids, many labile and variable structures whose development apparently depends on the physiological condition of the cell. These have therefore been discovered relatively

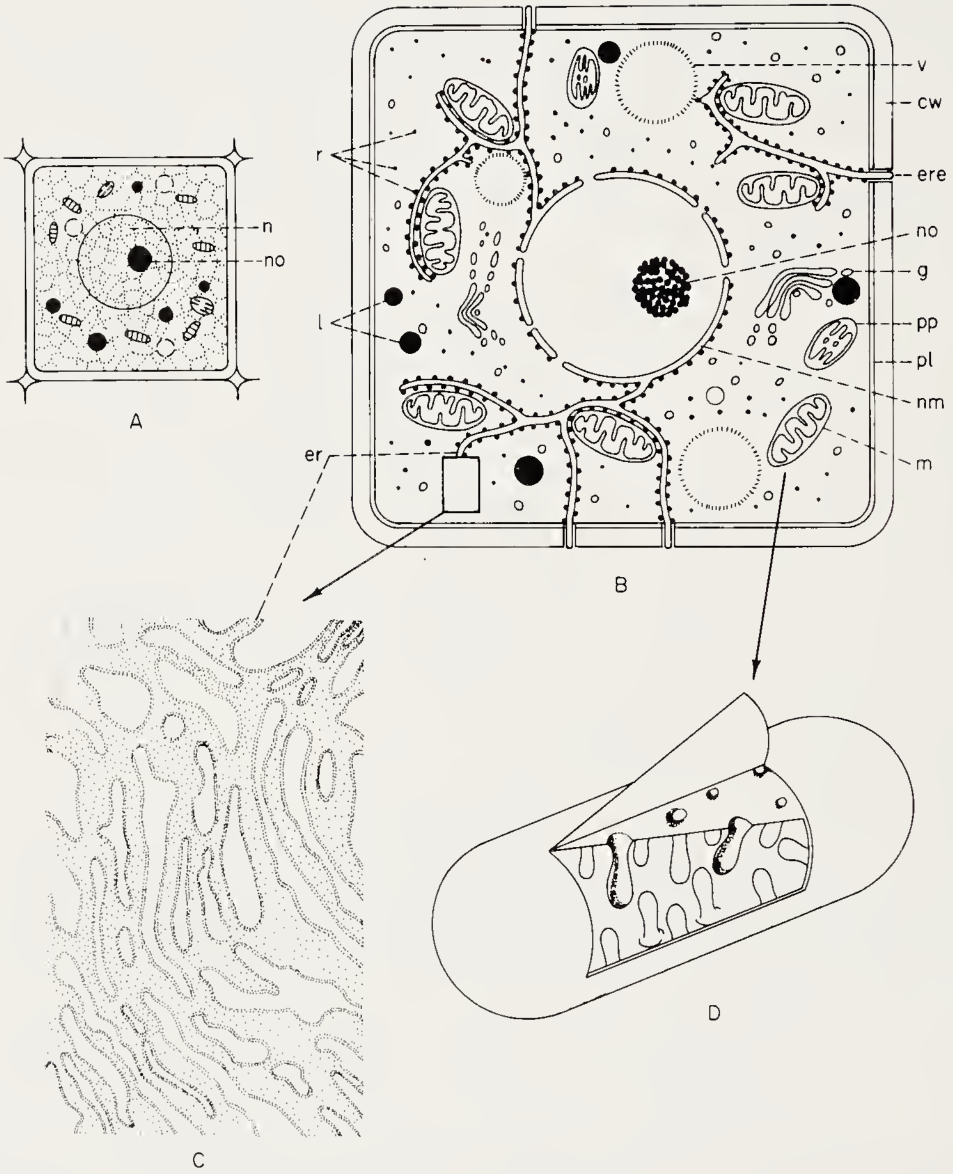


FIG. 3.1. Schematic diagram of a meristematic (embryonic) plant cell. (A) Under light microscopic resolution; (B) under electron microscopic resolution; (C) endoplasmic reticulum, drawn from an electron micrograph, cisternae not labeled (see Fig. 3.2); (D) model of a mitochondrion (tubular type) with the front cut away. In the upper part the outer membrane is slightly folded back. cw, Cell wall; er, endoplasmic reticulum; ere, endoplasmic reticulum evagination (probably not continuous through the cell wall but corresponding to a simple pit in the cellulose wall); g, (dictyosome) Golgi bodies; l, lipid droplets; m, mitochondrion; n, nucleus showing chromatin network; nm, nuclear membrane; no, nucleolus; pl, plasmalemma; pp, proplastid; r, ribosome; v, vacuole.

late even with the electron microscope. The protoplasts of neighboring cells are normally connected by thin plasma threads, the *plasmodesmata.*

ENDOPLASMIC RETICULUM

The endoplasmic reticulum (ER) has so far been found only in cells possessing true nuclei (see pp. 55–56). Its extent, in any case, depends very strongly on the physiological condition of the cell. Occasionally marked changes can be observed within only a few minutes. It interlaces the cytoplasm as a multiple, intercommunicating system of channels which can widen into crevices or cisternae (Fig. 3.1B,C). Its "walls," which appear dark on shadowing in the electron microscope, are built from membranes, while the inner space appears light and is apparently filled with a fluid, probably a mixed aqueous phase. The ER has therefore been regarded as a transporting system, which quickly transmits certain products from their place of synthesis to their place of utilization. It could possibly have further functions such as the synthesis or condensation of materials. Evaginations of the ER or protoplast, as plasmodesmata, penetrate the pits of the cell wall and connect neighboring cells (Fig. 3.1B). Often, though not always, small organelles, the ribosomes, are lined up on the outside of the ER. These are sites of protein synthesis, as shall be further explained below.

GOLGI APPARATUS

A Golgi apparatus is found with great regularity in the cytoplasm of cells with true nuclei. The term "Golgi apparatus" is presently used not for the network-like structures in animal nerve cells first described by Golgi but for the sum total of the dictyosomes. These are flat voids (cisternae) bounded by membranes and stacked in layers (Figs. 3.2 and 3.3). The cisternae occasionally appear angular in cross section, or bent in the shape of a horseshoe (Fig. 3.1B), apparently perforated like nets. In the active condition, small bubbles, the so-called Golgi vesicles, are pinched off from their edges (Figs. 3.2 and 3.3). The origin of the dictyosomes is still uncertain. Several observations support the idea of propagation by fragmentation of the cisternae, although there is also some evidence for other types of formation.

The function of the Golgi apparatus is not yet clear in all cases. Since an accumulation of dictyosomes has been observed in many dividing

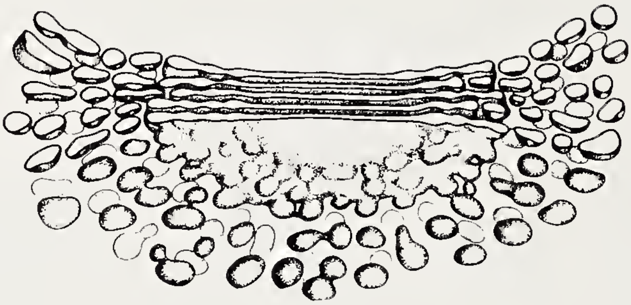


FIG. 3.2. Reconstruction of physiologically active dictyosomes. Five flat cisternae with numerous pinched off Golgi vesicules. (After Drawert.)

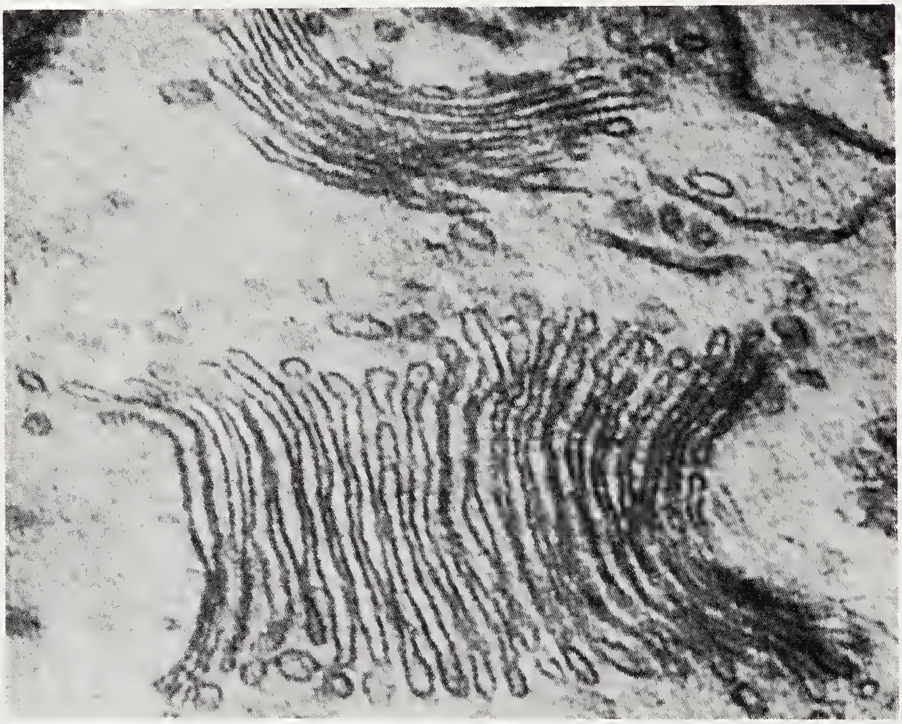


FIG. 3.3. *Euglena gracilis.* Electron micrograph of thin sections of two dictyosomes cut in different planes. Vesicles can be seen at the edges of stacked lamellae. Fixed in $KMnO_4$, magnification about 75,000×. (Original micrograph by Dr. W. Könitz.)

cells in numerous objects near the newly-formed cell walls, it is reasonable to assume that one of its tasks is the provision of cell wall material. In secretory cells producing slime (see p. 92), their task is the production and secretion of slime which consists of acid polysaccharides.

The production of essential oils also seems to take place in the dictyosomes. Quite generally, it could be said that accumulations of dictyosomes occur in places of intensive synthetic activity.

PLASMALEMMA OR PLASMA MEMBRANE

Plasmalemma is the term used to describe the "unit membrane" (biomolecular lipid leaflet or the 2 protein, 1 lipid layers of Danielli) which form the true outer boundary of protoplasts (Figs. 3.1B and 3.6E). It acts as a physiological barrier controlling the entry and excretion of substances (see pp. 32–33). Many types of cells have a plasmalemma with an extracellular carbohydrate-rich coating, e.g., walls of plant cells and the cuticle of insect epithelia.

MICROSOMES

Originally this name used to include all granular enclosures of the cytoplasm which could not be clearly identified in the light microscope. Today the term "microsome fraction" is understood to cover all plasma enclosures and fragments of plasma structures which sediment from the homogenized tissues when cells are destroyed by homogenizing followed by ultracentrifuging at accelerations of 50,000–100,000 g (g is the acceleration due to gravity). This fraction too is heterogeneous and contains various particles some of which have not yet been identified. The microsome fraction includes ribosomes, which consist of 40–60% RNA, proteins, and some other organic compounds. They are either distributed throughout the cytoplasm or, as has already been mentioned, lined up on the surface of the endoplasmic reticulum (Fig. 3.1B). As we now know, the ribosomes are the sites of protein synthesis (see p. 312).

Mitochondria (Chondriosomes)

The mitochondria (Fig. 3.1B,D), which occur in all cells with true nuclei (see p. 55) are easily distinguishable from the microsomes described above by their size and structure. They are mostly one to several microns long and have diameters in the range of 0.5–0.8 μ. Our knowledge of their fine structure is again due to the electron microscope.

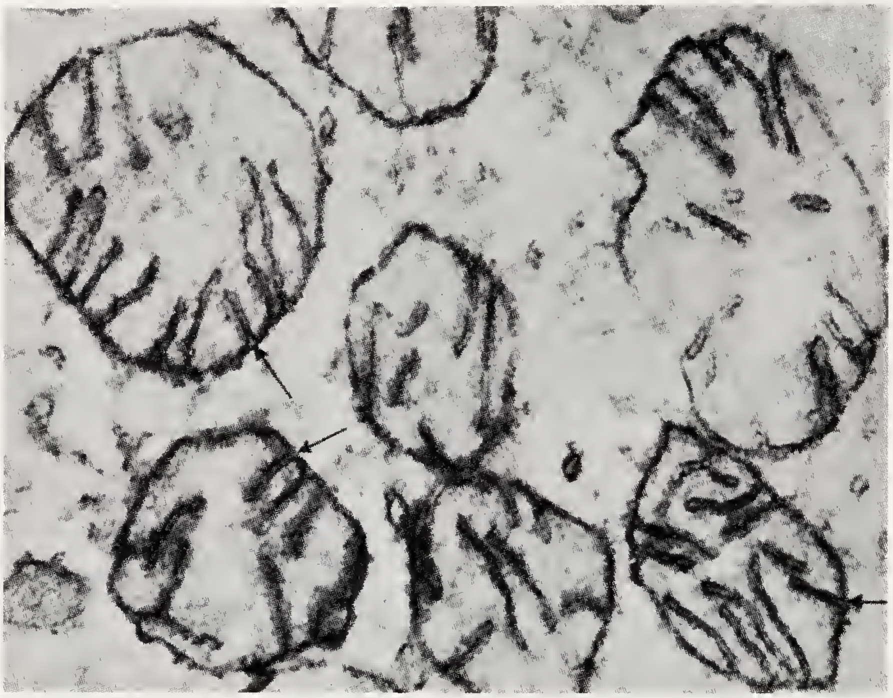


FIG. 3.4. *Euglena gracilis.* Electron micrograph of ultrathin sections through mitochondria in various planes. The arrows point to the places where invagination of the inner membrane is clearly visible. Fixed in $KMnO_4$, magnification approx. 45,000×. (Original micrograph by Dr. W. Könitz.)

They are separated from the protoplasm by a double membrane. Inversion of the inner membrane gives rise to folds (cristae), tubules (tubuli), and sacs (sacculi) (Figs. 3.1D and 3.4). Between the outer and inner membrane there is a gap which is probably filled with a fluid. Functionally, the mitochondria are carriers of respiratory enzymes especially the enzymes of the Krebs cycle, the respiratory chain, oxidative phosphorylation (see pp. 231–232), and fat metabolism. The strongly developed internal surface is also apparently connected with this function; the enzymes are regarded as being localized on these surfaces.

By means of negative staining it has recently become possible to demonstrate the presence of short-stemmed round particles about 80–100 Å in diameter in electron micrographs of mitochondria. These are located mostly, if not exclusively, on the inside of the inner membrane. Experiments in which the particles were mechanically separated from the membranes have indicated that at least a part of the respiratory enzymes is located in them. They have therefore been called *oxysomes.* Lately, however, not only their function as enzyme complexes but even their existence *in vivo* has again been questioned.

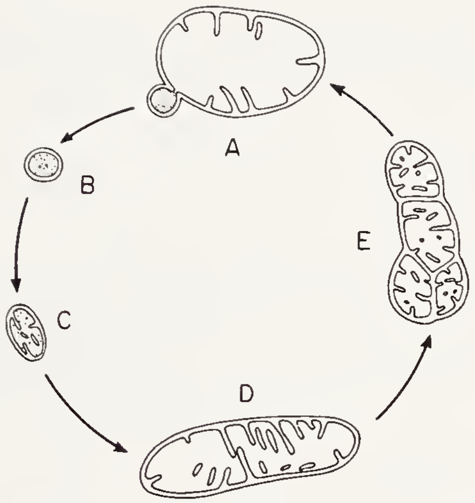


Fig. 3.5. Cycle of mitochondrion development on *Splachnum ampullaceum* (schematic). (A) Mitochondrion with "bud"; (B) pinched-off mitochondrion precursors; (C) promitochondrion with incipient differentiation; (D) fully developed mitochondrion; (E) mitochondrion division. (After von Maltzahn and Mühlethaler, adapted.)

The mitochondria can intersect, iris diaphragm fashion, in a direction perpendicular to their long axes (Fig. 3.5E). In the course of cell division they are divided between the daughter cells produced. Some authors believed that they can also be produced from precursors, the so-called *promitochondria;* these are bounded by double membranes and have a diameter of approximately 500 Å. They are thought to originate from the pinched-off "buds" from fully differentiated mitochondria and to develop inward folds, i.e., cristae or tubuli, by the extension of the inner membrane (Fig. 3.5A–D). The promitochondria too can be passed on from cell to cell. The average number of mitochondria is estimated to be a few hundred per cell.

Other Inclusions

Some further particles have also been found in the plasma which are known as *spherosomes, cytosomes,* and *lysosomes.* These are round or oval shaped with diameters in the range of 1–1.5 μ. The views as to their chemical nature, their fine structure, and function are still very divergent. The spherosomes are mostly lipid droplets, which are strongly osmiophilic, i.e., store OsO_4. They can also be surrounded by a unit membrane. Cytosomes are bounded by single membranes and are built of fine granular basic substance. Finally, the lysosomes are remarkable for their high content of enzymes, i.e., acid phosphatases.

Plastids

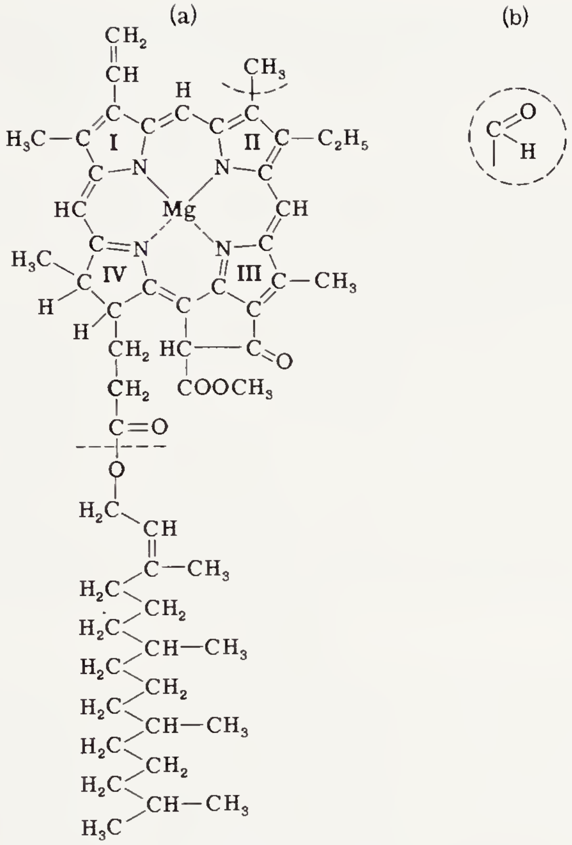
Plastids are characteristic cell organelles of all autotrophic plants (see p. 193); with the exception of the Cyanophyceae and the bacteria, they exhibit photosynthetic activity. We can distinguish, according to their color, the green *chloroplasts*, the yellow to orange *chromoplasts*, and the colorless *leucoplasts*. The first two groups are also known collectively as chromatophores.

In spite of the differences in structure and in function, the plastids represent a single type of organelle, since on the one hand the various types of plastids are interconvertible and on the other hand they develop from common precursors, the *proplastids*. These are surrounded by a double membrane and are at first undifferentiated. On cell division, they are distributed between the daughter cells. When proplastids develop into chloroplasts the inner membrane folds in (Fig. 3.1B) and so gives rise to the characteristic thylacoids (see pp. 50–51). Plastids, like mitochondria, can also propagate by division by way of a simple constriction (Fig. 3.6A).

CHLOROPLASTS

These are the organelles of photosynthesis (see p. 204) and so the carriers of the photosynthetically active pigments, the chlorophylls and carotenoids.

Chlorophyll a, like hemoglobin, consists of a porphyrin ring system in which four pyrrole rings are joined to each other by methane groups (see formula). In the center there is a magnesium atom held by coordination bonds, in the place of iron in heme. On the third pyrrole ring there is a five-membered isocyclic ring whose carboxyl group is esterified with methyl alcohol. Apart from these, the following side-chains are also present: four methyl, one ethyl, and one vinyl group, as well as a propionic acid residue esterified with the long-chain alcohol phytol ($C_{20}H_{39}OH$). *Chlorophyll b* differs from chlorophyll a only in that the methyl group on the second pyrrole ring is replaced by an aldehyde group (see formula). In any case, chlorophyll b does not occur in all photoautotrophic organisms. Several groups of algae, such as the



Chlorophyll a and b

Cyanephyceae, Diatomeae, Phaeophyceae, and Rhodophyceae contain no chlorophyll b. In recent years some further chlorophylls (c, d) have been discovered, but these occur only in certain plant groups. Of special interest, on the other hand, is bacteriochlorophyll (2-acetyl-devinyl-3,4-dihydrochlorophyll) which occurs in photoautotrophic bacteria.

Carotenoids are yellow, orange, or red lipid-soluble pigments (lipochromes) whose structure is based on the framework of carotene ($C_{40}H_{56}$); the latter is built up from eight isoprene units. The carotene molecules contain no oxygen; this is shown for instance by β-carotene, which occurs regularly in the chloroplasts, and by α-carotene, which differs from the former only by the position of one of the double bonds. Oxidative cleavage of β-carotene in the middle of the molecule results in two units of vitamin A. β-Carotene is therefore the provitamin A for mammals. The *xanthophylls* contain oxygen as hydroxyl groups; examples are lutein ($C_{40}H_{56}O_2$) (dihydroxy-α-carotene) which occurs in the chloroplasts, and fucoxanthine. Fucoxanthine occurs in certain algae (Diatomeae, Phaeophyceae) in such large quantities that it masks the chlorophyll and imparts a brown color to the chromatophores; these are therefore known as phaeoplasts. More than 70 carotenoids are now known.

Apart from the pigments discussed above, certain other chromoproteins, the biliproteins, also participate in photosynthesis in Cyanophyceae and Rhodophyceae. One can distinguish the reddish-violet *phycoerythrin* and the blue-green *phycocyanin*. These are responsible for the red color of the rhodoplasts and the blue-green color of the Cyanophyceae.

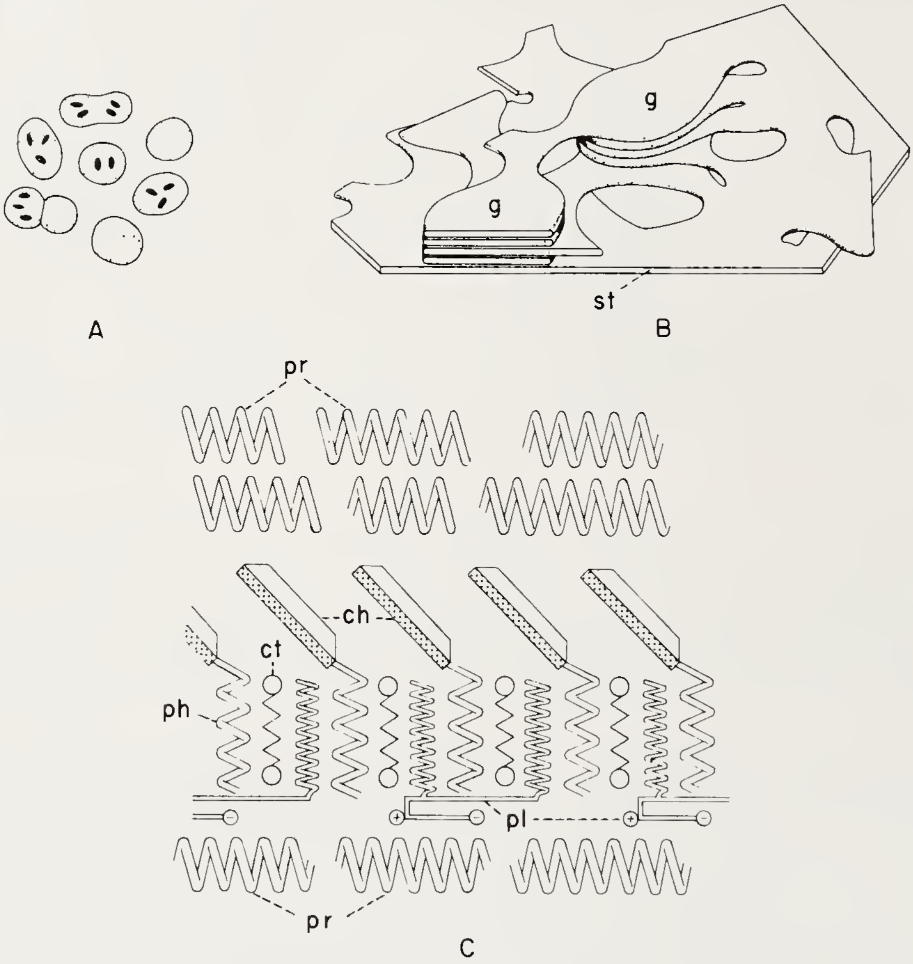
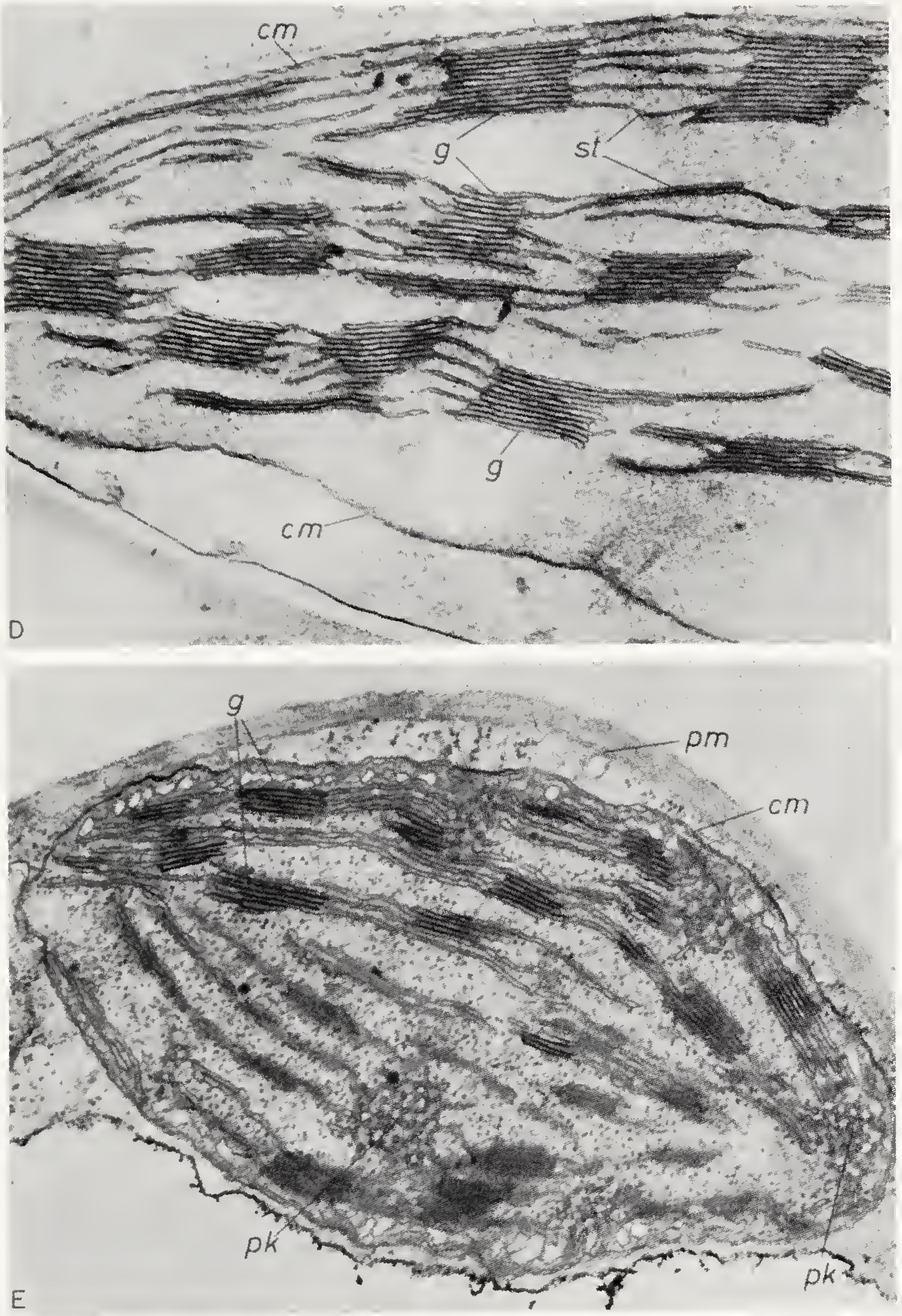
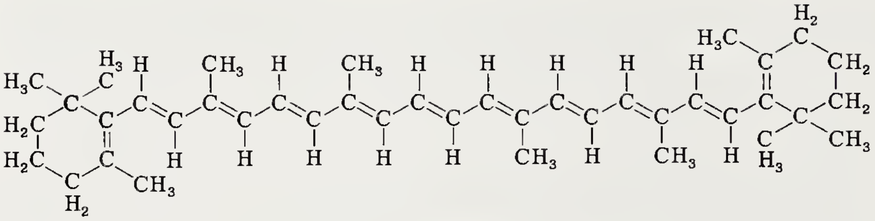


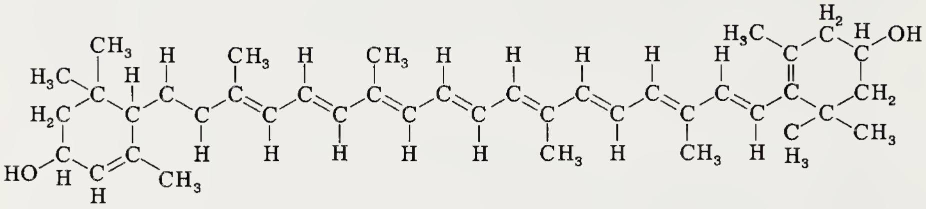
Fig. 3.6. Chloroplasts. (A) Single chloroplasts with starch grains, partly in the process of division (approx. 1000×); (B) schematic drawing of a membrane corpuscle with two stacks of grana. In the foreground is the section of a grana area (after Wehrmeyer, adapted); (C) hypothetical scheme of molecular arrangement in thylacoid membranes (after Calvin); (D) electron micrograph of a thin section through a chloroplast in spinach (grana type). Fixed in $KMnO_4$, magnification



approx. 27,000× (original micrograph by Dr. W. Wehrmeyer); (E) electron micrograph of a thin section through a chloroplast of *Zea mays* (maize) with prolamellar corpuscle (pk) and ribosomelike stroma particles. Fixed in glutaric dialdehyde-OsO$_4$ (approx. 36,000×). (Original micrograph by Dr. W. Wehrmeyer.) ch, Porphyrin ring system of chlorophyll; cm, chloroplast membrane; ct, carotenoid; g, grana area; ph, phytol residue; pk, prolamellar corpuscle; pl, phospholipid; pm, plasmalemma; pr, protein, and st, stroma thylacoid.



β-Carotene



Lutein

While the chloroplasts in higher plants are generally lens-shaped (Fig. 3.6) and have diameters in the range of 4–8 μ, those in algae exhibit many different forms. Apart from small granule-shaped chloroplasts, similar to those in higher plants, the chromatophores can be plate-shaped (Fig. 3.7A) helically winding bands (Fig. 3.7B), wound in loops (Fig. 3.7C), perforated like a net (Fig. 3.7D), stellate (Fig. 3.7E), or of some other shape. Each algal cell contains, as a rule, only one or two of the large chromatophores and correspondingly more of the smaller ones. For higher plants only orders of magnitude can be given. Thus, a mesophyll cell contains on the average about 50 chloroplasts, while their number in the terminal cells of stomata is usually less than 10.

After a longer exposure to light the chloroplasts contain small particles of assimilated starch (paramylon, Fig. 3.6A). Unlike the chloroplasts of higher plants, algal chromatophores can contain special centers, the pyrenoids Figs. 3.7A–E and 3.8B) for the production of reserve substances (starch, fats).

The fine structure of the chromatophores can only be resolved in an electron microscope. As can be seen in Figs. 2.5 and 3.6D and E, the chromatophores are separated from the surrounding cytoplasm by a double membrane. Their basic substance is known as the *stroma*. The stroma is stratified by numerous membranes known as *thylacoids* which

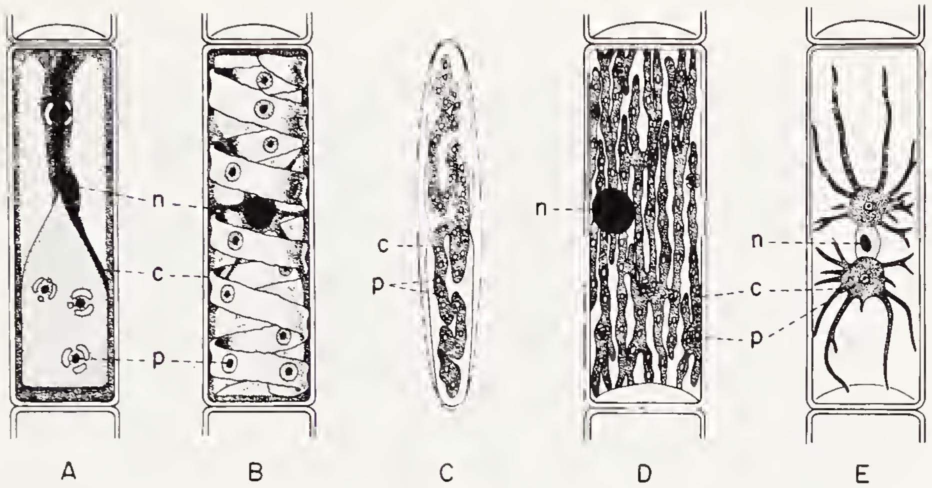


Fig. 3.7. Algal chromatophores. (A) *Mougeotia* sp. Plate-shaped chromatophore; its upper part is rotated through 90° from the flat to the edge on position (approx. 500×); (B) *Spirogyra* sp. (approx. 200×); (C) *Pleurosigma angulatum,* band-like aspect (approx. 200×); (D) *Oedogonium* sp. (approx. 500×); (E) *Zygnema* sp. (approx. 650×). c, Chromatophore, n, nucleus; p, pyrenoid, partially surrounded by starch granules. (After Palla, Kienitz-Gerloff, Karsten, Schmitz, adapted.)

describe their specific functions and molecular structure (see below). Various types of chromatophores can be distinguished according to the arrangement of the thylacoids.

The algal chromatophores are lamellar throughout, i.e., the thylacoids penetrate the chromatophores longitudinally (Fig. 3.8A). As shown by Fig. 3.8B, they also enter the pyrenoids and form together with a relatively dense osmiophilic basic substance the so-called pyrenophore. The number and the arrangement of thylacoids in the pyrenophores appear to vary with the physiological condition of the cell. In the pyrenoids of starch-producing algae, the starch (in *Euglena,* the starchlike paramylon, see p. 24) is deposited at the edge of the pyrenoids (Figs. 3.7 and 3.8B).

The grana-type chloroplasts, which are characteristic of higher plants, reveal a different thylacoid arrangement in the electron micrographs of thin sections. As is shown by Fig. 3.6D, short thylacoids whose length corresponds approximately to the diameter of optically just resolvable *grana* (known therefore as granathylacoids) alternate here with longer ones. These latter continue on one or both sides of the grana domain in the so-called intergrana region of the stroma and are known as stromathylacoids. The *granathylacoids* are stacked on top of each other in characteristic "stack of coins" arrangements. According to recent investigations it seems that sterically the grana and the *stromathylacoids* form a coherent membrane tissue in which the granathylacoids are joined to

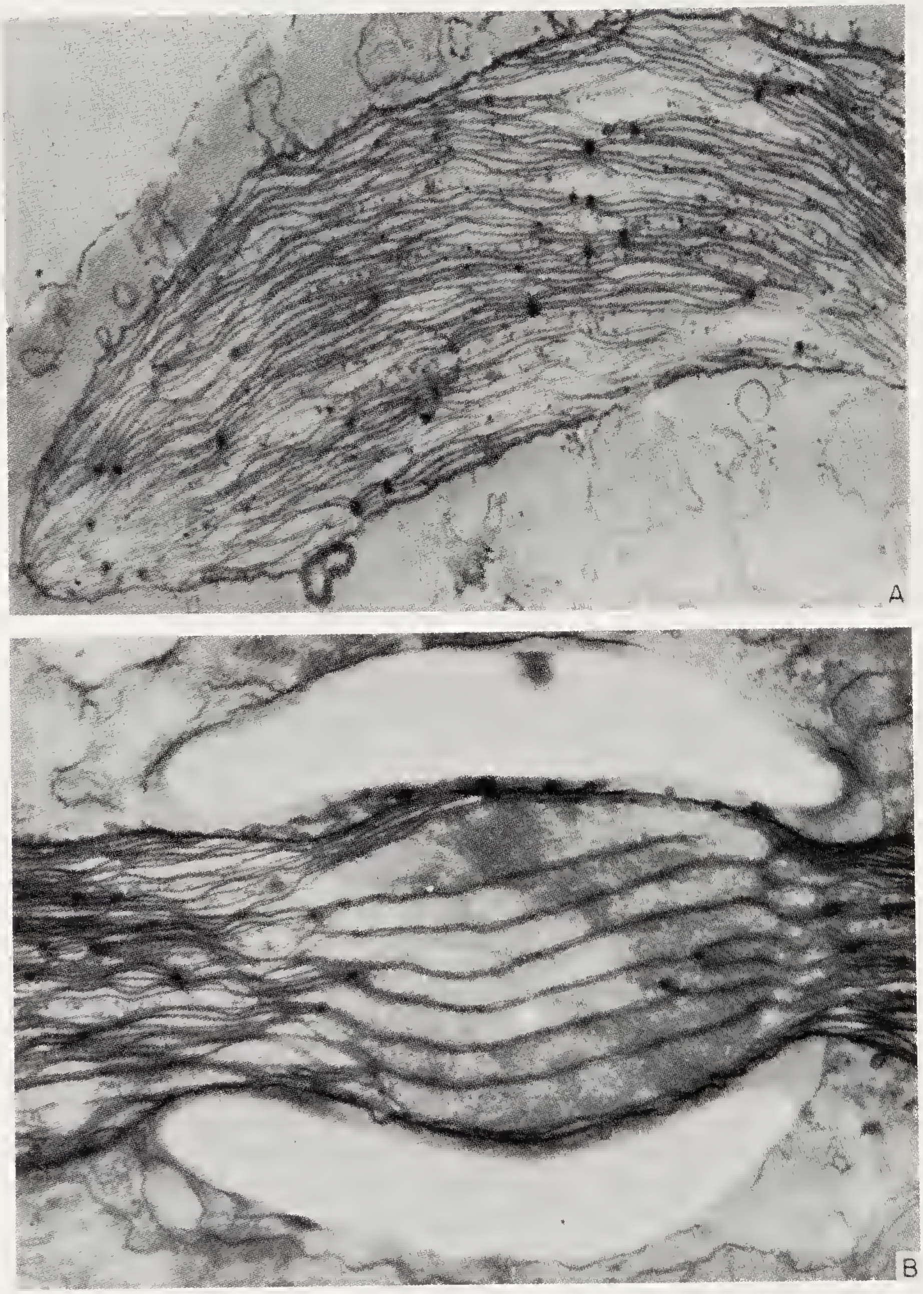


FIG. 3.8. *Euglena gracilis.* Electron micrographs of ultrathin sections: (A) of a chloroplast (of fully lamellar type); (B) of a pyrenoid. The paramylon has been dissolved during the preparation, but the original positions can still be recognized as cavities surrounded by membranes. Fixed in osmium tetroxide. Lead shadowing. Magnification approx. 40,000×. (Original micrograph by Dr. W. Könitz.)

the thylacoids of the intergrana region and through these to each other by narrower or wider joints (Fig. 3.6B).

In etiolated plants (see p. 352) raised in the absence of light there develop instead of the normal thylacoid membranes the so-called *prolamellar corpuscles* of tubular crystal lattice structure. On exposure to light the crystal lattice structure collapses and reforms as granathylacoids. Secondary production of prolamellar corpuscles can also be brought about by temporary exclusion of light from already green plants, as is shown by the chloroplast of *Zea mays* in Fig. 3.6E.

While the thylacoids of algal chromatophores are covered with pigment molecules over their entire surface, the pigments of grana-type chloroplasts seem to be limited to the granathylacoids. In any case it is still not definitely clear whether, at least in some cases, the pigments could be located on the stromathylacoids.

With regard to the structure of the thylacoid membranes at the molecular level, there is as yet no universally accepted view, although there are several indications that the chlorophyll, as shown in the hypothetical scheme in Fig. 3.6C, covers the lipoprotein membranes as a monomolecular film. Since at least some carotenoids can transfer the absorbed light energy to the chlorophyll (see p. 205) they must be closely associated with the chlorophyll molecules. One possible arrangement is shown in Fig. 3.6C. Recently some authors have advocated the view that the lipoproteins, chlorophylls, carotenoids, and other substances taking part in the photosynthetic process (see p. 204) are joined in photosynthetic elementary units, the so-called *quantasomes*. Electron micrographs show these to be of approximately spherical shape with diameters of about 100–180 Å. Their molecular weight is given as two million.

The occurrence of nucleic acids in chloroplasts is now regarded as certain. Whether they too function as messengers has not yet been established, but it is likely (see p. 319). Sometimes ribosomelike particles (Fig. 3.6E) can be recognized on electron micrographs of chloroplasts in the stroma.

CHROMOPLASTS

The chromoplasts colored yellow, orange, or reddish due to their carotenoid content contain no chlorophyll and arc photosynthetically inactive. They occur in correspondingly colored flowers, e.g., in pansies (*Viola tricolor,* Fig. 3.9A) and nasturtiums (*Tropaeolum*), in fruits (tomatoes), and in other plant organs, e.g., carrots (*Daucus carota*).

Round, oval, spindle-shaped, and irregular ameboid forms are known (Fig. 3.9B). In the light microscope, carotenoids appear more or less evenly distributed in the stroma, concentrated in droplike globuli or as crystals (rhombs, needles, etc.). Apart from the crystalline and globular types of chromoplasts, fibrillar submicroscopic elements can also be seen in electron micrographs. The crystals can become so large that they are only surrounded by a thin chromoplast sheath which can finally be broken. The chromoplasts develop either directly out of proplastids or by transformation from chloro- or leucoplasts. During the transformation of a chloroplast into a chromoplast, the membrane corpuscle is decomposed.

LEUCOPLASTS

These are free of pigments and occur in many colorless plant organs, especially in storage organs (bulbs, rhizomes, piths) where they take part as *amyloplasts* in the formation of reserve starch. Their function has not yet been clarified in every case.

The Cell Nucleus

The nucleus or karyon[1] is separated from the cytoplasm by a more or less distinct boundary, the *nuclear membrane,* and can generally be recognized in the light microscope without special staining. It is most frequently spherical but sometimes appears flattened into lens-shape, ellipsoidal, or in some other shape. Its size is distinctly, but not strictly, related to the mass of the surrounding cytoplasm (cytonuclear ratio) and is therefore extremely variable. Its diameter is often of the order of 5–25 μ, but diameters of some hundreds of microns also occur. The nucleus, which refracts light more strongly than does the cytoplasm, appears homogeneous in the light microscope. The nucleus, fixed and stained with basic dyes and as viewed by the phase-contrast microscope, reveals a networklike structure. In the past this has been referred to as the *chromatin* or nuclear reticulum (Fig. 3.1A), due to the ease with which it could be stained. The threads of this reticulum are elongated chromosomes (see p. 57) which appear to be randomly coiled in the

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[1] The term "karyon" is used only in composite words such as karyoplasm and prokaryosis.

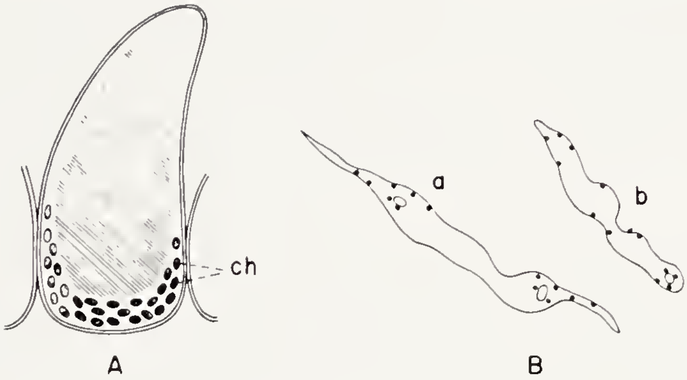

Fig. 3.9. (A) Papilla from the epidermis of a petal of pansy (*Viola tricolor*). The cell sap (shaded) is colored by anthocyanins. In the lower half of the cell there are many chromoplasts (ch). Magnification approx. 200×. (B) Ameboid chromoplasts from the epidermis of the red berries of lily of the valley (*Convallaria maialis*); (a) and (b) show the active change of form of the same chromoplasts within 5 minutes. The globuli in which the dyes are concentrated are shown as dark dots surrounding single vacuoles; approx. 2000×. [After Steffen (1964).]

nucleus. The remaining volume of the nucleus is filled with an apparently structureless substance, the *karyolymph*. Finally, nuclei contain one or more *nucleoli* which can also be intensively stained with basic dyes. These are characterized by their RNA content.

Nuclei with the characteristics given above occur in plant cells at every stage of evolution except in bacteria and Cyanophyceae. These two groups possess DNA-containing structures equivalent to nuclei but without their typical structural features (see p. 104); the above organisms are therefore described as *prokaryons*, as distinct from the so-called *eukaryons* which have "true" nuclei. On the other hand, there are also plants whose cells contain more than one nucleus. Since, however, every nucleus has it own sphere of influence in the plasma, even in the absence of a dividing cell wall, the assembly of nuclei and plasma are here no longer equivalent to a single cell; this is expressed by the concept of "*cenoblast*." Each physiological unit of such a cenoblast, which consists of a nucleus and its sphere of influence in the plasma, is known as an *energid*. A cenoblast is therefore polyenergid. Morphologically and in size, a cenoblast can wholly correspond to a normal plant cell, e.g., in the green alga *Cladophora* (see p. 116). However, the cenoblasts can also be tubular and reach sizable dimensions as in the Phycomycetes (see p. 114) and in the Siphonales (see p. 114).

While most of our knowledge of the structure of the cytoplasm is due to the electron microscope, our knowledge of the structure of the nucleus has not so far been appreciably extended by the use of this instrument. The nuclear membrane appears as a double membrane in electron micrographs, and it is apparently part of the endoplasmic reticulum with which its inner space is connected (Fig. 3.1B). The existence of pores connecting the inner volume of the nucleus with the cytoplasm is also indicated (Figs. 2.5 and 3.1B). The content of the nucleus, the karyoplasm, appears granular in the electron microscope, but the granules are apparently not randomly distributed in the karyoplasm but often appear to be arranged as helices of various sizes. There can hardly be any doubt that they correspond to the helically wound fibrous elements of the chromosomes (see below), but a proof of their identity is hard to come by.

Chemically the nucleus is characterized by its high DNA content compared with other cell organelles; the DNA is located in the chromosomes. From the point of view of its functions, it is the carrier of the genetic material (genes) and is therefore the genetic control center of the cell (on plasma genetics see p. 317). It carries out its functions in the state described above, which has previously been called by the misnomer "resting nucleus"; it would be better described as the interphase or a "working nucleus." As its function requires that the genetic information it contains should be passed on completely and without alteration from cell to cell, division of the cell is typically connected with a characteristic morphological change of the nucleus in which the chromosomes appear as self-contained units.

CHROMOSOMES

The chromosomes owe their name to the ease with which they can be stained with basic dyes (see above). During the division of the nucleus they assume the shape of relatively short, compact rods, mostly curved or angled (Figs. 3.10A and 3.11). Sometimes, however, they are so short that they appear almost spherical (Fig. 3.11). The *centromere* (also known as the kinetochore or spindle attachment region) is found at the knee-bend, which appears somewhat constricted; it connects the two limbs of the chromosome which are often of unequal lengths. Many chromosomes also exhibit secondary constrictions, which serve to separate certain sections of the chromosomes (Fig. 3.10A). These are sometimes very small and when terminal are known as satellites. Satellites are connected with the rest of the chromosome by filaments in which the chromonemas (see below) are not wound helically. The DNA is therefore poorly identifiable by staining in these sections so that it appears as if there were no DNA there at all. For this reason they are known as SAT regions (sine acido thymonucleinico), but not quite correctly since the corresponding chromosomes known as SAT chromosomes give rise to nucleoli. In general, a chromosome consists of a pellicle or nuclear membrane enclosing homogeneous karyolymph in which is suspended a pair of coiled chromonemas.

The division of chromosomes occurs by longitudinal cleavage into a pair of so-called *chromatids.* In most cases the longitudinal duplication can be observed long before the final cleavage, but the separation occurs only on division of the centromere. The daughter chromosomes produced in this manner are alike both with respect to their shape and to their gene content.

The structural and functional units of the chromosomes are the *chromonemas.* According to the original definition, this name describes the helically wound elongated elements of the chromosomes that can just be resolved in the light microscope (Fig. 3.10A). Each daughter chromosome (homologue) formed during division must contain at least one such chromonema, which is exactly duplicated before the cleavage into chromatids. In this instance the terms chromatid and chromonema are synonymous when the nucleus and each chromosome contains a single (haploid) set of genes in one chromonemata. However, there are indications that in many cases the chromosomes contain a larger number of chromonemata. Thus, each chromatid may characteristically consist of two subunits, the half chromatids. In some cases the number of chromonemas is apparently still larger (16 or 32), and in the so-called giant chromosomes in the salivary glands of *Diptera* and certain plants their number amounts even to multiples of 16 or 32 (polyteny, Fig. 3.10E).

With the aid of special fixing and staining methods the presence of small, intensively stained, regions can be shown on the chromonemas. These are known as *heterochromatin* or *chromomeres* and are lined up on the chromonema like strings of beads. The arrangement of the chromomeres, which can easily be distinguished by size and to some extent also by form, is characteristic of each chromosome and is identical in the two parallel, elongated, elements of one and the same chromosome. In the giant chromosomes too they are located in each strand at equal height, so that they create the impression of bands or disks (Fig. 3.10E). The earlier views according to which genes occurred exclusively in the chromomeres, or even that each chromomere corresponds to a gene, had to be given up after genes have been found in euchromatic regions between the chromomeres as well. Today it is believed that the appearance of stained chromomeres is caused by a tighter helical winding of

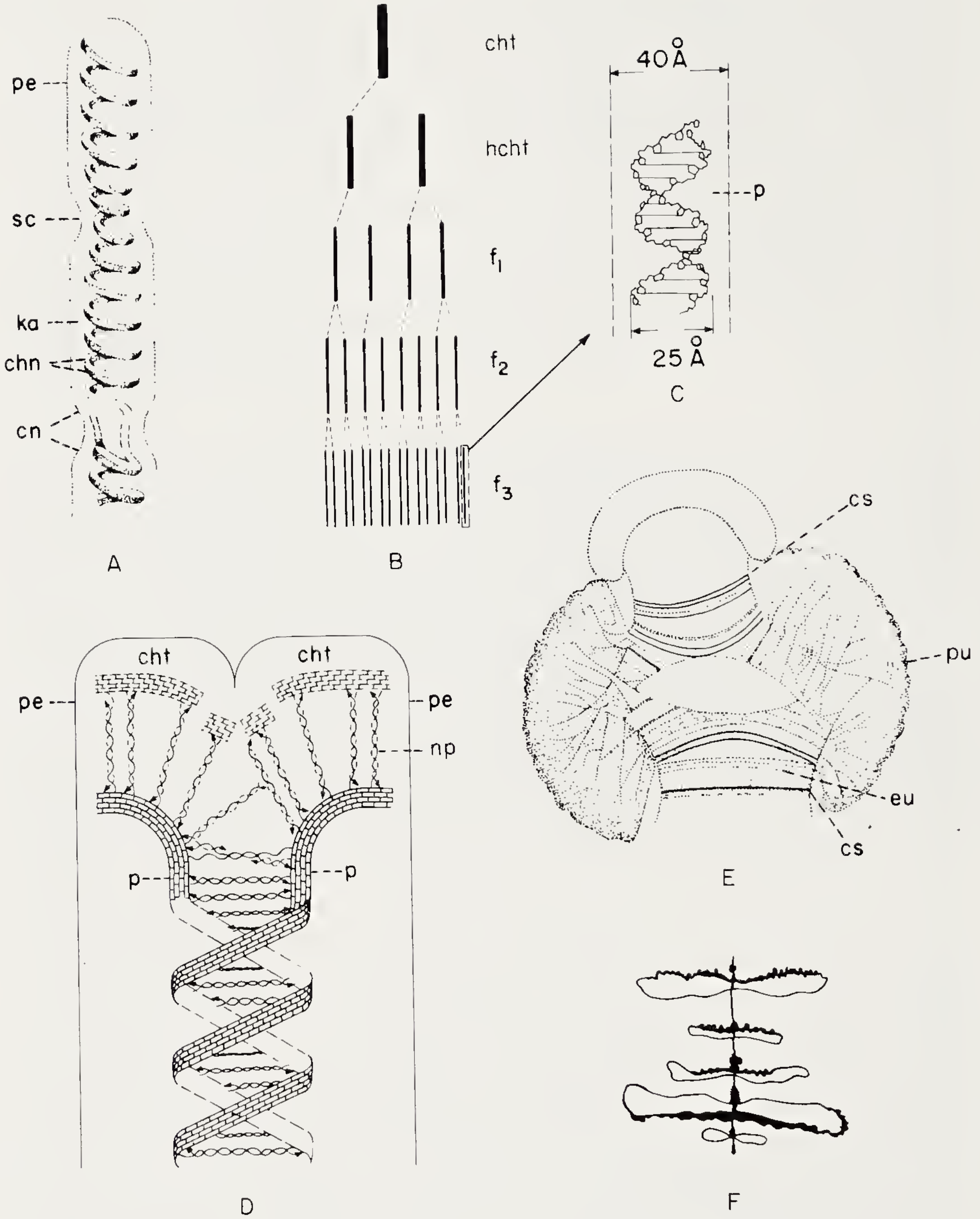

FIG. 3.10. The structure of chromosomes. (A) Schematic picture of a chromosome showing a thickened membrane or *pellicle* (pe), clear fluid matrix or *karyolymph* (ka); coiled paired strands of chromatin or *chromonemas* (chn); the spindle attachment region known as the primary constriction, kinetochore, or *centromere* (cn) whose structure is very ambiguous; and one nonterminal *secondary constriction* (sc) which helps to identify certain sections of the chromosome. (B) Fine structure of chromatids according to the multistrand hypothesis. cht, Chromatid; hcht, half-chromatid; f, 200-250 Å fibrils; f_2, 100-125 Å fibrils; f_3, 30-40 Å fibrils. (C)

the chromonemas in the respective places or by local development of loops (see below). Chromosomes or chromosome sections are heterochromatic if, on staining, they become much more intensively colored than the normal euchromatic ones. However, the difference between euchromatin and heterochromatin is probably not qualitative but quantitative, in that the elongated elements of the heterochromatic sections are wound tighter and are also richer in phospholipids and certain nucleic acids. On the other hand, the lack of DNA in the SAT regions seems to be connected with a marked extension of the helices.

When a chromosome changes from the compact form highly suitable for movement about the cell at the end of nuclear division into the relaxed and extended form found in an interphase nucleus, the chromonemas stretch and unwind. They then appear as irregularly wound long threads. When compressed into a relatively small volume by the development of the nuclear membrane, they appear as an irregular nuclear reticulum on which the chromomeres can be distinguished as easily stained particles. The heterochromatic sections usually remain, even in the active nucleus, in easily stainable regions, the so-called chromocenters.

Views on the fine structure of the chromosomes are still very divergent. The electron microscope has resolved fibrillar elements of helical appearance both in the *karyoplasm* of the interphase nucleus and in the chromosomes in various stages of division. These can be grouped into classes of different size, which are approximately the same in the karyoplasm and in the chromosomes. Helices 200–250 Å thick are rather common, and are therefore regarded by many authors as the true structural elements of the chromosomes, but they themselves are composed

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40-Å fibril, consisting of a DNA helix with a protein (p) sheath (schematic). (D) Hypothetical model of the division of a chromosome (daughter chromosome or homologue) into two half-chromosomes or chromatids (cht) by the intrusion of the pellicle (pe) between paired chromonemas which are cleaving; also, each chromatid or chromonema (single DNA strand) is in the process of replication (synthesis) to form half-chromatids. The arrows show the free ends of the nucleic acids strands wound around each other in opposite directions. The other ends rest on the opposite protein strands (p). The protein and DNA elements newly built in during division are shown by broken lines. (E) Part of a giant chromosome with a puff (pu) (see p. 335) and dark-staining heterochromatin (chromomere disks) (cs) and light-staining (euchromatic) (eu) portions of the chromonematal strands. Most of the "genes" seem to be located in the chromomere portion of the nuclear strand. (F) Part of a lampbrush chromosome with loops emerging sideways from the central thread (schematic). (Partly redrawn after Steffenson, De, Baermann, Gall, and Callan.)

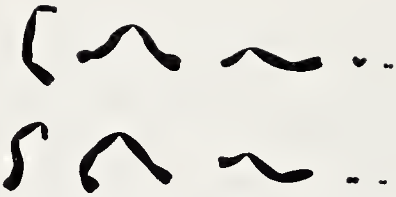

Fig. 3.11. A diploid set ($2n$) of the metaphase chromosomes of *Crocus hiemalis.* The five homologous pairs are drawn above each other. (Redrawn after Darlington.)

of still finer fibrils, the finest of which have diameters of 30–40 Å. This corresponds approximately to the diameter of a DNA molecule surrounded by a sheath of histones and protamines (Fig. 3.10C).

While the existence of such fibrils in the nucleus and in the chromosomes can therefore be regarded as established, our ideas on their arrangement in the chromosomes are still only hypothetical. According to the so-called multistrand hypothesis, the individual fibrils, starting with those 40 Å thick, are wound around each other in pairs (Fig. 3.10B); this would explain the existence of the various size groups. The individual fibrils are thought to be cross-linked by ionic bonds via Mg and Ca. The single-strand hypothesis, on the other hand, considers only a single elongated element wound as a multiple helix and giving rise to windings of primary, secondary, and higher orders.

One model which explains many cytological, biochemical, and genetic findings is shown in Fig. 3.10D. According to this model a chromatid consists of a double protein helix; the DNA and histone-protein strands are arranged perpendicular to the long axis of the helix and parallel to one another. The replication of the chromonemas could occur by cleavage of the double helix starting at its ends with simultaneous synthesis of the complementary nuclei acid strands. At present it is not possible to say which of the various hypotheses and models is correct, and further intensive studies will be required before either of the models described above can be regarded as even partly substantiated.

Certain conclusions about the structure of chromosomes can also be drawn from the so-called lampbrush chromosomes which have been found to occur in many families of animals and in some plants. The lampbrush chromosomes develop in the meiotic prophase during the pairing of homologous chromosomes (see p. 266). As shown by Fig. 3.10F, the central strands carry side loops produced by the protrusion of the elongated elements, which in due course are drawn in again. Apparently this is a form assumed by chromosomes for special functions, in which the normally compact structure is loosened by the development of loops. However, many authors regard them as larger-sized equivalents of normal chromosomes. Thus, for example, chromomeres could develop in the chromonemas by the development of loops of this kind.

Since the number of chromosomes per cell is constant for any given species, and since, moreover, the chromosomes in their division forms assume a very definite shape that is no way affected during the stages of division, one is wholly justified in speaking of chromosome individuality. In any case, the chromosomes occur in pairs with respect to size and shape in every normal body cell (Fig. 3.11). These pairs are known as *homologous chromosomes* and have at any given time the same chromomere pattern. The cells of the body therefore typically contain two homologously paired sets of chromosomes of similar shape; they are therefore *diploid.* As a single set of chromosomes, which occurs in *haploid* cells, is denoted by the letter n, the diploid cells can be characterized by the symbol $2n$.

NUCLEAR DIVISION

As has already been mentioned, according to the findings of classic cytology a cell is always derived from another cell with division of the parent cell nucleus. This division cannot occur directly, i.e., by a simple constriction; such violent separation of the chromosomes could never insure an even distribution of the *gene* material between the two daughter cells. There is a clear-cut relationship between *genes,* the sites of "genetic information" and specific portions of the DNA double helix (chromonema) in the chromosomes. The nuclear division of vegetative cells is known as *mitosis.* First, chromosomes are transformed into the already described division form. This is followed by duplication of chromonema, the formation of chromatids and their even distribution between the daughter cells, and finally by reappearance of the "active" or interphase nucleus. In this way each daughter cell ends up with the same chromosome complement.

The course of mitosis, which usually lasts for about one-half to two hours, is usually subdivided into several *phases* illustrated by characteristic figures (Fig. 3.12). It must be remembered, however, that these are arbitrary divisions of a continuous process into certain stages, and that the figures represent snapshots of a dynamic event and not resting periods between the individual stages.

Prophase (Fig. 3.2/1–4)

The division of the nucleus begins with helical winding and shortening and thickening of the chromonema, duplication of chromonema, and

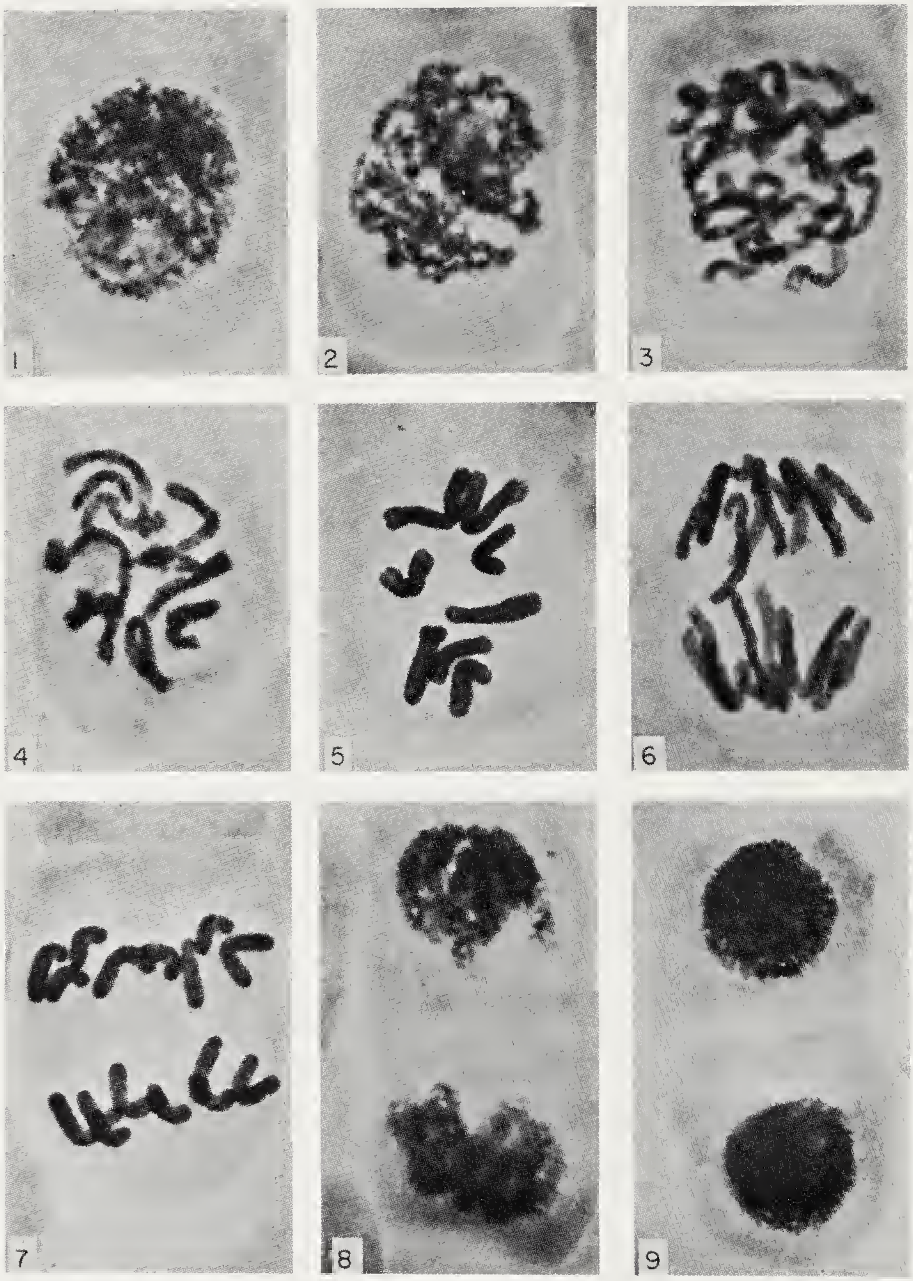

FIG. 3.12. Mitosis in the root tip of *Bellevalia romana* (*Hyacinthus romanus*), a plant with nearly euchromatic chromosomes. 1, Nucleus in the interphase or a beginning prophase; 2–4, prophase; 5, metaphase (polar view); 6–7, anaphase; 8, telophase; 9, daughter nuclei. [From Oehlkers (1956).]

cleavage of each into two chromatids. The nuclear membrane starts to break down and is dispersed in the other elements of the endoplasmic reticulum. Toward the end of the prophase the nucleoli break down, too, and RNA is released into the cytoplasm. At the cell poles the polar caps may be distinguished; these poles are the points of convergence of the nuclear spindle fibers. Centrosomes, which are widespread in the animal kingdom, occur in only a few groups of plants as a modified mass of cytoplasm, related to the spindle apparatus, which become the polar caps.

Metaphase (Fig. 3.12/5)

The helical winding process of the chromosomes into their most compact form is completed during the metaphase. When completed, the spindles consist in part of *continuous fibers* extending from one pole to the other, and partly of *traction fibers* which are attached to the centromeres of the chromosomes and extend to one pole. The chromosomes are arranged in the so-called equatorial plane of the cell.

Anaphase (Fig. 3.12/6–7)

In the anaphase the cleaved half chromosomes separate and with the centromere in front migrate to the two poles. Our ideas on the mechanics of this process are still insufficiently clear. Some observations indicate that the chromosomes are being "pulled" toward the poles by the shortening of the traction fibers which consist of contractile proteins. This process consumes ATP. The possibility of active chromosome self-propulsion or streaming, electrostatics, viscosity, hydration, etc., of the cytoplasm cannot, however, be excluded.

Telophase (Fig. 3.12/8–9)

This phase comprises a conversion of the chromosomes from their compact form into the extended chromonema: strands characteristic of the prophase of the chromonema. Duplication into two strands can often already be recognized at this time. The nuclear membrane is reformed, presumably from parts of the endoplasmic reticulum, which already concentrate at the poles at the end of the metaphase, and move in between the chromosomes during the anaphase, finally joining up in a nuclear membrane. The nucleoli are reformed; the SAT chromosomes serve here as nucleolus organizers. A relatively dense, hyaline zone, cylindrical to barrel-shaped, the so-called *phragmoplast*, is now produced from *continuous* fibers across the center of the dividing cell. Golgi vesicles, built from the nearby dictyosomes, accumulate in the equatorial plane; these carry acid polysaccharides—the structural units of the basic material of the cell wall. These coalesce to form the *cell plate*, a clear sol layer in which primary cell wall materials are deposited, which starts from the center, and finally intersects the side walls to divide the cell. The vesicle membranes coalesce and form the plasma membrane in the daughter cells on both sides of the cell plate. At the places where the endoplasmic reticulum intercepts the cell plate no primary wall forms, leaving a primary pit area; this leads to the formation of *plasmodesmata*, protoplasmic extensions through the primary cell wall to the permeable intercellular substance.

Mitosis seen as a whole therefore consists of two normally coupled but independent processes: identical replication of the chromonema which leads to the duplication of chromosomes, by longitudinal cleavage into chromatids; and regular distribution of the cleavage products between the two daughter cells. The fundamental independence of these processes is indicated by the so-called *endomitoses*, in which doubling of the chromosomes occurs inside the nucleus. The nuclear membrane remains intact and no spindles are produced. Such endomitoses occur in normally diploid plants mainly in tissues exhibiting increased metabolic activity, and lead to cells with 4, 8, etc., up to 256 or more sets of chromosomes which are known as tetra-, octo-, etc., or polyploid cells. Such somatic polyploidy, affecting only certain tissue regions of a plant, should not be confused with normal diploidy in which already the embryonic cells (and therefore all body cells derived from them) contain at least two sets of chromosomes due to fusion of sperm and egg nuclei (see p. 266).

The Cell Wall

Most plant cells, as distinct from almost all animal ones, are surrounded by a rigid cell wall.[2] The only plant exceptions are the naked plasmodia of the Myxomycetes, certain flagellates, and lower fungi in their ameboid developmental stages. The cell wall is essential for plant cells because, when fully developed, it encloses a cell sap vacuole (see p. 74) which is surrounded only by a thin layer of cytoplasm. As the concentration of the cell sap is higher by about one order of magnitude than that of the surrounding medium, the cell would continue to absorb water and finally burst as a result of osmotic pressure if the swelling were not opposed by the counterpressure of the cell wall.

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[2] The sometimes encountered expression "cell membrane" is not recommended; the term "membrane" is nowadays used mostly to describe plasma membranes (see above), and this could easily lead to misunderstanding, e.g., in the case of the cytoplasmic membranes of bacteria (see p. 105).

All cell walls in the bodies of plants, with the exception of the cuticle covering the ovule, have been produced as dividing walls in a late stage of mitosis. The cell wall is, therefore, a product of the synthetic activity of the protoplasts. However, because of its special structure and composition it can carry out certain functions even after the death of the protoplasts; it can, for instance, contribute to the plant's rigidity. Corresponding to the diversity of their tasks, both the structure and the chemical composition of cell walls vary considerably. Owing to shortage of space, the following presentation must be limited to the essentials.

Microscopic and Submicroscopic Structure

In the light microscope the cell walls appear more or less stratified. The walls of neighboring cells are separated from each other by intercellular substance (Fig. 3.13A,B), which consists mainly of pectinlike materials and acts as intercellular cement joining the primary cell walls together. The cells later part at the corners and edges, become rounded off, and form air-filled gaps, the intercellular spaces (Fig. 3.13A). The intercellular substance is hardly visible, and can usually only be identified with the aid of special microscopic methods. It has a gellike character and consists apparently of discontinuous fibrous structural elements (Ca or Mg pectate), not revealed in the electron microscope, suspended in the homogeneous sol matrix of the old cell plate.

Before the cell plate is even completed and becomes attached to the sidewalls, the daughter cells begin to build the primary walls from both sides on the intercellular substance. The cell plate is therefore three-layered right from the time of its completion. The primary walls already contain hemicellulose, but as yet only in very small proportions. The elongated microfibrils are arranged at random (scattered texture, Fig. 3.13B) and are joined to form a loose network. Similar to the reinforcement in concrete, this network is embedded in a basic substance (matrix), which is chemically very similar to the intercellular substance and merges into it without a sharp boundary. As a result the primary wall is very elastic, but can also undergo plastic stretching and deformation and can thus accommodate the growing cell.

At about the end of the cell growth the primary wall may accumulate a second layer, the so-called secondary wall. The cellulose content of this

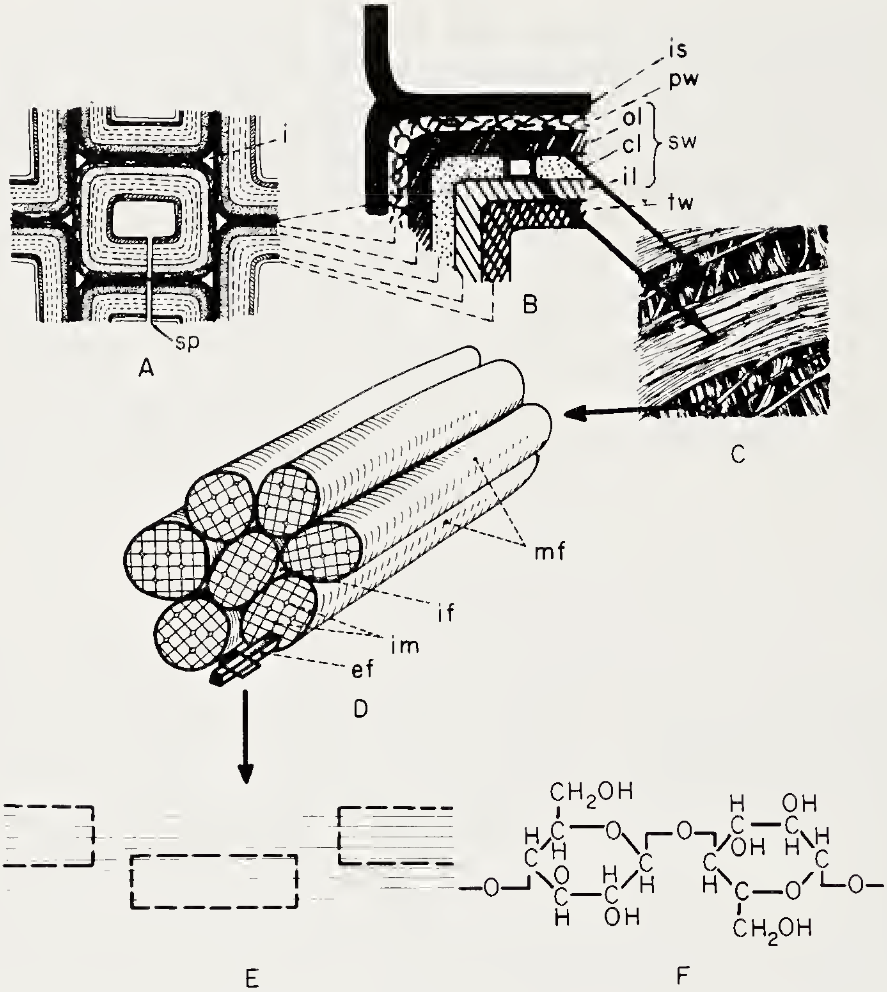


FIG. 3.13. Cell wall. (A) Schematic stratification of the cell wall, e.g., in pine. i, Intercellular space; sp, simple pit. (B) Plane projection of the individual layers: is, intercellular substance; pw, primary wall; sw, secondary wall, possibly consisting of: ol, outer layer, cl, central layer, il, inner layer; tw, tertiary wall. (C) Stratification of the secondary wall in the electron microscope (*Valonia*) showing changed orientation of cellulose fibrils in successive layers. (D) Bundle of several microfibrils, the cross section showing the micellar structure of single elementary fibrils (schematic) ef, Elementary fibril; if, interfibrillar space; im, intermicellar space; mf, microfibril. (E) Schematic drawing of the joining of cellobiose units into "micellar strands." (F) Bimolecular section (collobiose unit) of a cellulose chain.

wall can amount to 94%. The parallel texture of the cellulose fibrils, which can extend continuously over long stretches (Fig. 3.13C), is a characteristic feature of many secondary walls. If several layers are packed upon one another, the directions of the long axes of the fibrils usually cross over in neighboring layers (Fig. 3.13C). The secondary wall is either multilayered as in the green alga *Valonia* (Fig. 3.13C), or triple as in many tracheids and wood fibers in which one can distinguish an outer, a central, and an inner layer (Fig. 3.13A,B). The best developed layer is the central one which itself appears to be stratified on a submicroscopic scale; it accounts for the bulk of the cell wall material. The inside of the secondary cell wall in a few cases may be covered with a tertiary wall, having a rough surface which again contains a higher proportion of the pectic substances.

In the walls of fibrous cells, the direction of the long axes of the fibrils in parallel orientation is of decisive importance for the mechanical properties of the cell wall. When the fibers are arranged approximately parallel to the long axis, the texture is said to be fibrous (Fig. 3.14A). Such fibers, e.g., in ramie, flax, and hemp, have high tensile strengths but little ductility. More frequent is the helical structure (Fig. 3.14B), characteristic of wood fibers and tracheids in which the fibrils are wound in a more or less tight helix around the long axis of the cells. Many of these fibers, e.g., those of the cocoa palm, are distinguished by excellent ductility. The ring texture type (Fig. 3.14C) is rarer; here the arrangement of the fibrils is approximately perpendicular to the long axis of the cell, though it is possible that these too are really low helices.

The microfibrils which are visible in the electron microscope and have diameters of approximately 250 Å can further be subdivided into about 20 finer units 30–100 Å in diameter (Fig. 3.13D). These are known as elementary or unit fibrils (micellar strands), and consist of 50–100 cellulose macromolecules each; the latter are partly crystalline, forming

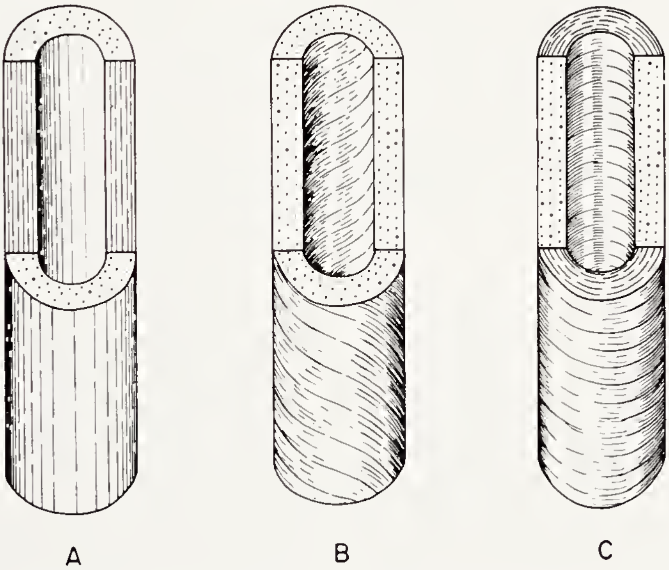


Fig. 3.14. Schematic sections of fibrous secondary walls showing different orientations of the cellulose fibers. (A) Longitudinal; (B) helical; (C) ring texture.

a chain lattice, and partly paracrystalline, i.e., parallel but not arranged in an ordered lattice. A cellulose molecule can belong simultaneously to both an ordered "micellar region" and to a paracrystalline region (Fig. 3.13E). This arrangement is known as "fringed micelles." Between the unit fibrils there are small cleavage spaces about 10 Å in diameter, which are known as intermicellar spaces. The microfibrils are separated by interfibrillar spaces, whose width is of the order of 100 Å. In the natural state the cell wall is swollen, i.e., both the interfibrillar and the intermicellar spaces are filled with water.

THE CHEMISTRY OF THE CELL WALL

As has already been mentioned (see pp. 22, 66), the macromolecules of cellulose consist of cellobiose units in which the glucose molecules are joined by β-glucoside linkages (Fig. 3.13F). The elongated zigzag-shaped macromolecules (see p. 22) can be of various lengths, depending on the degree of polymerization. The highest values found so far are about 8000 glucose units per molecule. Each glucose molecule occupies about 5 Å of space in the chain, which gives a mean chain length of about 4 μ. The chains in the natural state may be even longer, since partial breakdown of the molecule could be expected on dissolution.

By the action of the enzyme cellulase, which breaks the β-glucoside linkages, the cellulose molecules can be broken down to cellobiose, which, in turn, is split into glucose by the enzyme cellobiase. Cellulose is insoluble in most know solvents, but it is soluble in Schweitzer's reagent (ammoniacal cupric hydroxide) without destruction of the fibrous molecules. In concentrated sulfuric acid the cellulose molecules break down to glucose (saccharification of wood). In contrast to starch, cellulose reacts with iodine only in the presence of certain swelling agents, such as zinc chloride. Unhydrolyzed cellulose becomes blue to dark violet, while hydrolyzed cellulose becomes yellow on staining with zinc chloride–iodine.

The matrix in which the microfibrillar network of cellulose is embedded consists mainly of protopectin and of polysaccharides other than cellulose; these were previously known as hemicelluloses (cellulosans). One can distinguish the pentosans, the macromolecules of which consist of sugars with five carbon atoms (pentoses), e.g., xylose and arabinose, and the hexosans which consist of hexoses with six carbon atoms, such as mannose and galactose. These are constituents, among others, of plant mucilage. In other cases they act as reserve materials, like the so-called reserve cellulose consisting mainly of mannans. This can be found, for example, in the seeds of the date palm (*Phoenix dactylifera*).

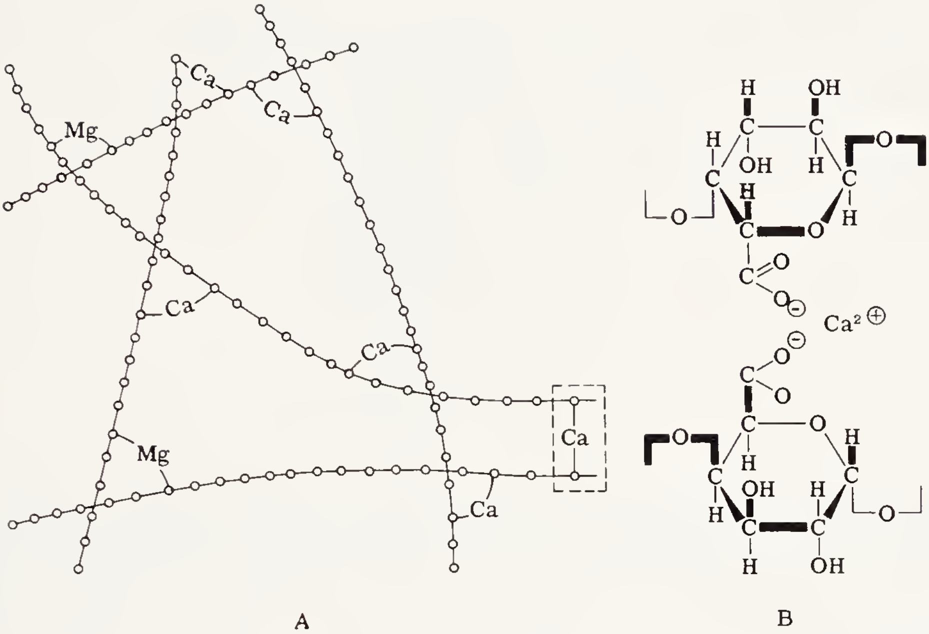
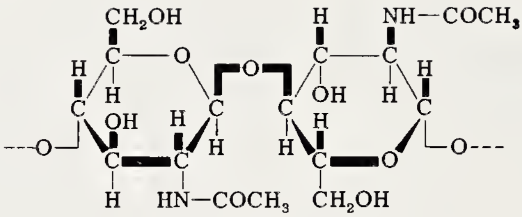


FIG. 3.15. (A) Cross-linking of pectin macromolecules through Ca^{2+} and Mg^{2+} ions. (B) Ca bridges. (Redrawn after Sitte.)

The macromolecules of pectins are composed of from 20 to 100 galacturonic acid molecules (Fig. 3.15). In protopectin they are cross-linked by having two carboxyl groups joined by two divalent ions, e.g., Ca^{2+} and Mg^{2+} (Fig. 3.15A,B). These bridges can be broken and reformed elsewhere relatively easily, which results in an elastic, easily variable network. Protopectin, which accounts for the bulk of the intercellular substance, can easily be dissolved in a mixture of potassium chlorate and nitric acid (Schulze's solution). The cellulose walls are not affected by this treatment; it is therefore possible to separate the cells of a tissue in this way (maceration). The intercellular substance can also be dissolved by the enzyme pectinase.

While cellulose is the typical skeletal substance of plants, there exist some plants, especially among the heterotrophic organisms, whose cell walls do not consist of cellulose. Apart from bacteria and Cyanophyceae, which were discussed elsewhere (see p. 105), the main examples are furnished by fungi. Although some of them have cellulose walls too, the walls of most fungi consist of fungal chitin; this macromolecule is built of acetylglucosamine units. These are also joined by β-glucoside linkages and form chain lattices similar to those of cellulose. The microfibrils in the fungus cell walls have approximately the same diameters (150–250 Å) as those in cellulose walls.



"A" Fungal chitin

PITS

Separation by a rigid cell wall would make the exchange of materials between neighboring cells very difficult and would isolate the protoplasts if there were no special connecting channels, the so-called pits. These are kept open during the period of primary growth of the cell by plasma bulges, which push the microfibrils apart (Fig. 3.16). If the cell walls become very thick from secondary wall deposition this leads to the formation of regular channels (Fig. 3.13A) by enzyme action. The closing membranes of the pits built essentially from the intercellular substance and the primary walls accumulated on both sides are perforated like sieves by fine plasma strands, the plasmodesmata. These

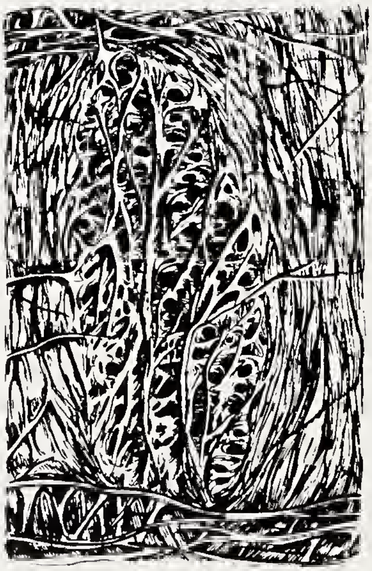


FIG. 3.16. Sketch of a pit in the primary wall of the *Avena* coleoptile. Transition from the mixed texture of the primary wall to the parallel texture of the secondary wall. (Drawing after an electron micrograph by Böhmer.)

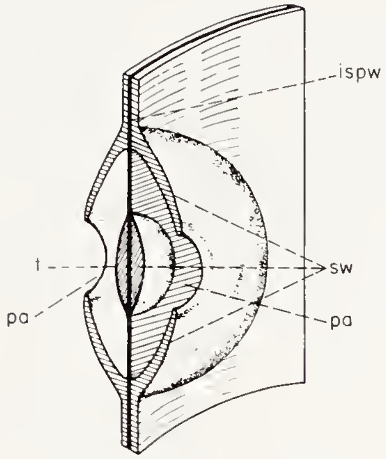


FIG. 3.17. Section across a bordered pit pair from tracheids of a conifer. ispw, Intercellular substance and primary wall (sometimes erroneously called the "middle lamella"; pa, pit aperture; sw, secondary wall; t, torus, secondary thickening on the primary wall.

allow the transport of materials from cell to cell and unify the plant organisms physiologically in spite of the spatial separation of the protoplasts. Each plasmodesma contains at least one strand of the endoplasmic reticulum.

A specific type of pit, the bordered pit, is characteristic of tracheary conduction channels. The relatively thick secondary cell wall around these pits overarches from one or both sides (Fig. 3.17) so that only a relatively small central pore pit (pit) remains open. In most conifers, Gnetales, and *Ginkgo* but rarely in angiosperms, this pore can be blocked like a valve by the *torus*. This is a central disc on the primary cell wall which has secondary thickening and which can be pressed against the pore by pressure from one side, and thus prevent the water columns moving up the stem from being broken.

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Chapter 4

Differentiation of the Cell

Differentiation and Primary Cell Types

Discounting the initially thin primary wall of the plant cells and the plastids, comparison of the characteristics of plant cells described so far reveals a certain similarity with animal cells, but this is only true of embryonic cells. The character of meristematic plant cells changes drastically with the onset of radial and longitudinal growth and of cell differentiation. This is due partly to the development of the cell sap vacuole, partly to the special characteristics of the cell wall, whose mechanical properties are very important for the performance of many cell functions, and partly to changes in cell contents. Vacuole formation and stretching of the cell wall arc two closely connected interdependent processes; both decisively affect cell enlargement through the action of a plant hormone, indole acetic acid. Moreover, the properties of the cell walls also can be altered by secondary wall accumulation and stratification. On the other hand, the character of many cells is also determined by the production of certain substances in the cytoplasm or the cell sap. The differentiation processes manifest themselves, therefore, both in the formation of certain morphological features and in the development of special physiological functions. All these changes are produced by the cytoplasm and its organelles, structures which can themselves undergo certain changes during differentiation.

The *differentiation* and concomitant specialization of the meristem cells result in the development of permanent primary cell types with specific functions quite different from the originally totipotent embryonic cells. Many differentiated cells with similar functions are normally combined in the plant body into complexes known as *tissues*. Basically, a distinction can be made between growing, undifferentiated, tissues (meristems) and permanent tissues. The former are embryonic tissues, capable of division either from the start of embryonic development or from permanent tissues in which the already differentiated cells regain (dedifferentiate) their power of division. Undifferentiated meristematic cells are totipotent, capable of giving rise to all other cell types. Among the permanent primary tissues one can distinguish, according to their functions, ground tissue giving rise to mature *parenchyma* cells of pith and cortex, protoderm giving rise to an epidermis, and procambial tissue giving rise to primary xylem and primary phloem. Depending on whether they were formed from primary (apical) or secondary (cambia) meristems, cells are described as primary or secondary. Several types of cells are sometimes described as tissue systems, e.g., xylem and phloem as a conducting system. Individual cells of different morphological and physiological characteristics are occasionally found in certain tissues; they are known as *idioblasts*.

Stages of Differentiation

Vacuolation and Protoplasmic Streaming

The first sign indicating the end of the meristematic phase and the start of the growth (cell division and cell enlargement) and differentiation processes is the formation of vacuoles. Until this time the whole cell has been densely cytoplasmic with only a few small vacuoles; now enhanced water uptake results in the formation of small water droplets (Fig. 4.1A). As these grow, they coalesce and give rise to a number of larger vacuoles (Fig. 4.1B) each separated from the cytoplasm by a typical membrane or boundary layer, the *tonoplast*. The whole vacuolar system is known as the vacuome. On continuing water uptake, the

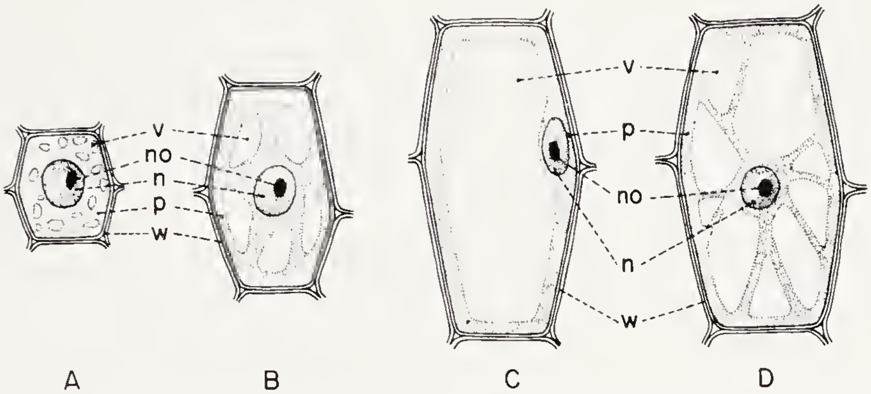

Fig. 4.1. Schematic formation of vacuoles: (A) cell at the beginning of expansion. Local dissociation of the cytoplasm to form small vacuoles; (B) expanding cell with many coalescing vacuoles; (C) cell at the end of expansion. The vacuole has pushed the cytoplasm back into a thin layer pressed against the wall; (D) as in C, but with the nucleus suspended in a plasma ventricle at the center of the vacuole. n, Nucleus; no, nucleolus; p, plasma (cytoplasm); v, vacuole; w, cell wall.

vacuoles finally either merge into a central cell-sap vacuole which almost fills the whole volume of the grown cell and presses the protoplasts against the cell wall in a thin layer and surrounds the nucleus like a utricle (Fig. 4.1C) or the vacuole space may be penetrated by a fine network of plasma threads suspending the nucleus in the middle of the central vacuole (Fig. 4.1D).

The shape of the network and the position of the plasma ventricle change continuously in the living protoplasm. Both are due mostly to cytoplasmic currents, which can be followed microscopically by observing the resultant movement of cell contents. The direction of the cytoplasmic flow can change and can be different in individual plasma strands and in the various regions of the plasma layer at the wall. This type of flow is known as protoplasmic streaming. In cells having only a thin peripheral protoplast lined up against the cell wall, the plasma current flows in only one direction along the cell wall. This type of current is known as the rotational current. Some other types of currents are also known, such as the multiple currents in slime molds where up to eight separate, alternating side-by-side flow patterns have been described. In many objects the plasma currents occur without visible outward signs, while in other cases they are caused by external factors (see p. 391). In the spring, vacuolation proceeds as described (Fig. 4.1B–D), in the winter the pattern is reversed (Fig. 4.1D–B).

The protoplast is separated from the vacuole by a plasma membrane known as the *tonoplast*, which must not be confused with the outer plasma membrane, the *plasmalemma*. Both membranes are to some extent selective, and since the cell sap contains many dissolved substances, the plant cell is an osmotic system. When the osmotic pressure of the cell sap is higher than that of the surrounding medium, as is normally the case with plants, the cell takes up water until the counterpressure produced by the tension of the cell wall (turgor) is sufficient to bring this process to an end (see p. 179).

The substances produced by the protoplasts can reach considerable concentrations, which could lead to very high osmotic values, but some of these substances are converted into osmotically inert forms, such as insoluble precipitates, or condense into macromolecules. Many of these substances are reserve materials, which can be mobilized at any time, i.e., brought back into solution. Others are secretions, i.e., metabolic products, for which the plant apparently has no further use. These are either deposited in the cell sap or, as in the case of gland cells, are secreted externally. From the chemical point of view these materials are very varied, corresponding to the manifold synthetic activities of plants. Only a few important groups can therefore be discussed below as changes in cell contents during differentiation; others shall be dealt with in more detail under secondary plant materials (see pp. 217–221).

CHANGES IN CELL CONTENTS

Storage of Reserve Materials

Although reserve materials can occur in variable quantities in practically every cell as products of the primary metabolism, the role of the storage of materials is often taken over by certain cells, especially in the parenchyma cells of pith and cortex. The reserve materials in these cells can accumulate to the extent of practically filling the whole cell.

Secretion and Cell Content Materials

While a steady exchange of gaseous substances occurs in both plants and animals, the excretion of metabolic products in solid or dissolved forms which is so important for animals has no significance for plants. If they occur at all, such substances are typically deposited as secretions in the vacuoles of certain cells or other cavities, without having any further obvious value for the plant. However, cells or even whole organs functioning as glands are also found in plants capable of excreting materials into the environment.

Carbohydrates (see pp. 8–10)

The most important reserve substances are the carbohydrates. They can be dissolved in the cell sap, like the monosaccharides glucose and fructose (widespread in fruits), or like the disaccharides maltose and sucrose (cane sugar). The latter occurs in large quantities in sugarbeet and sugar cane. However, carbohydrates occur more frequently as polysaccharides, which can be stored in any large quantities without danger of osmotic damage. *Starch,* the typical plant reserve carbohydrate, can, for instance, accumulate to form up to 70% of the fresh weight (Fig. 4.2). The starch grains can be stratified concentrically or excentrically, can be round, oval, or some other shape, and can be single or multiple (Fig. 4.3). In oats, starch can be composed of several hundred single granules. The formation of starch granules occurs in the *leucoplasts,* which are also known as amyloplasts due to their role in starch synthesis. The layering is produced by the alternation of regions of lower and higher density; the regions of high density are located on the inside of each layer. In the potato, two or three layers are formed every day. The stratification is concentric when the amyloplast surrounds the starch granule as a uniformly thick layer. When the center of starch synthesis is not located in the middle of the amyloplast, the granule appears excentrically layered. Amylose and amylopectin both occur in native starch (see pp. 22–23). The presence of starch can be shown by iodine: The iodine molecules penetrate the helical starch molecules (see p. 23), which leads to strong absorption of visible longer wave radiation, i.e., to a blue-violet color. Dextrins are obtained by partial decomposition of the starch molecule into shorter chains.

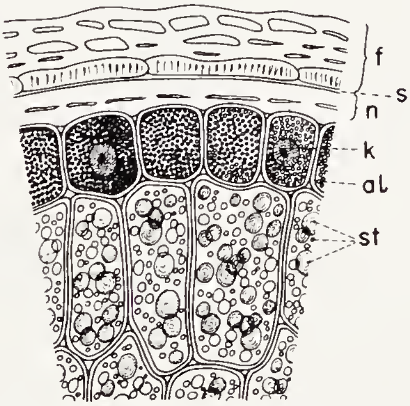

FIG. 4.2. Cross section of a wheat grain, approx. 200×. al, Aleurone; f, pericarp; k, nucleus; n, nucellar layer; s, testa; st, starch granules. (After Strasberger, modified.)

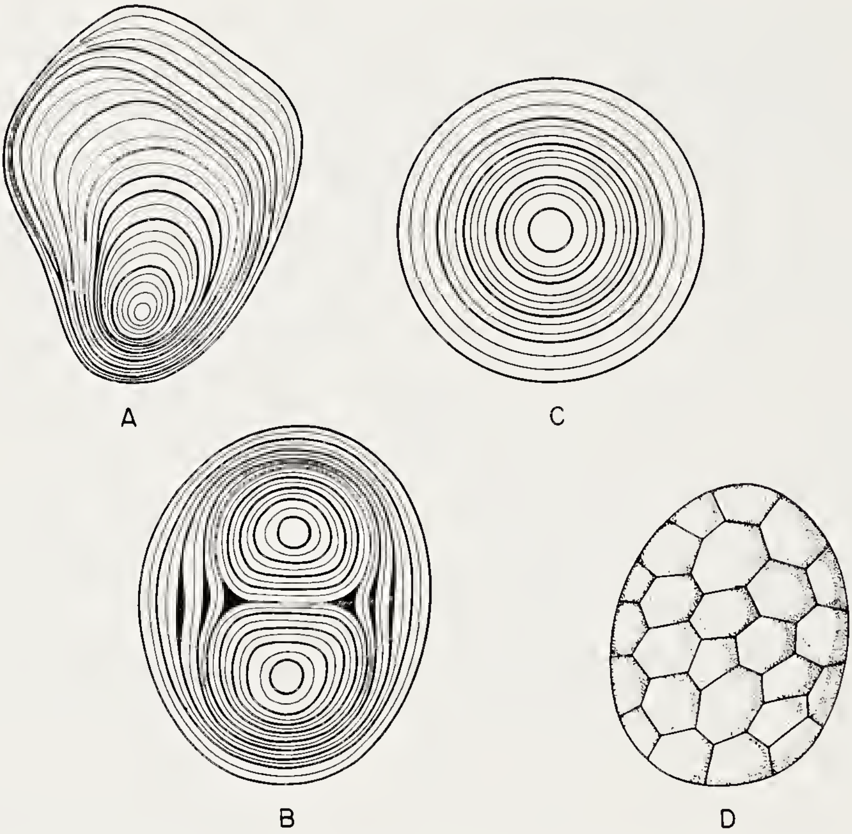

FIG. 4.3. Starch grains: (A–B) potato starch [(A) single; (B) composite]; (C) wheat starch; (D) oat starch. (After Kny and Gassner, modified.)

Other reserve carbohydrates occurring in plants are the already mentioned reserve cellulose *inulin* such as found in *Inula helenium* (inula) and *Helianthus tuberosus* (artichoke), and glycogen (see p. 24). The latter is the typical reserve material of bacteria, fungi, and the Cyanophyceae. The inulin molecule is built up from fructose units, so that artichokes can be used as potato substitutes for diabetics, whose diet often contains fructose as well.

Proteins

Proteins too are widespread reserve substances. They are either dissolved in the cell sap, or occur as solid crystalloids or as approximately spherical aleurone grains, which are protein vacuoles solidified by dehydration. They occur in large quantities in the aleurone layer of cereal grains (Fig. 4.2), which is separated from ordinary flour and remains in the bran, but included in wholemeal bread. The aleurone grains consist mainly of globulins. The cells of the flour endosperm also contain proteins in the form of so-called gluten, which determines the baking qualities of the flour. It consists essentially of glutelins and gliadins.

Fats and Oils

The fats and oils are important mainly in many algae and in the oil-rich seeds of some higher plants (flax, rape, *Ricinus*, sunflower, groundnuts, etc.) in which they can account for over 50% of the dry matter. The fruit pulp of olives is also very rich in fats. The fats are either emulsified into small droplets or coalesce into larger oil drops or homogeneous fatlike substances.

Salt Crystals

Apart from numerous salts which occur as solutes in the cell sap, crystals of sparingly soluble salts often occur in plant cells. These crystals are mainly calcium carbonate and calcium oxylate; the latter can occur in monoclinic or hexagonal single crystals, druses, raphids, or as microcrystals (Fig. 4.4), while calcium carbonate occurs mostly in the form of small crystals.

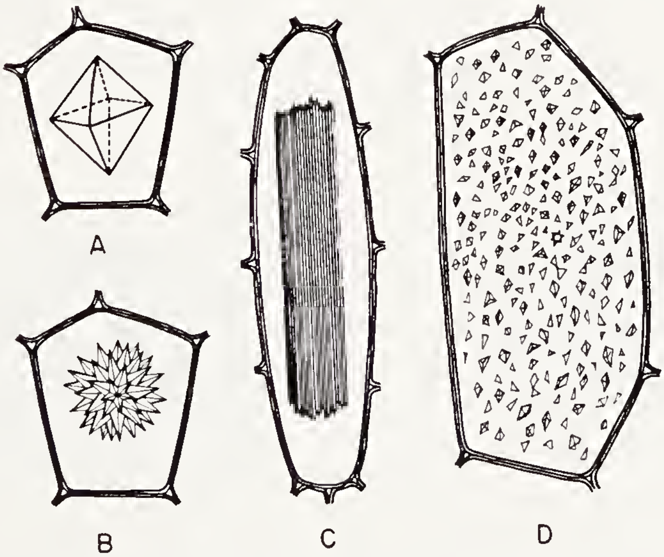

FIG. 4.4 Oxalate crystals, ca. 400×. (A) Single crystal; (B) druse; (C) raphids; (D) microcrystals. [After Troll (1959, p. 144), modified.]

Pigments

Apart from the pigments bound structurally in the chromatophores and taking part in photosynthesis, there are also many pigments that are soluble in the cell sap. These impart characteristic colors to certain plant organs, as in many flowers (Fig. 3.9A) and in crimson-colored leaves (copper beech, etc.). The blue, violet, or red shades are due to anthocyanins, the yellow ones to flavones. Both are secondary plant materials (see p. 218).

Latex

A characteristic secretion of certain plants (e.g., *Euphorbia* and dandelion) is the milky sap (latex) contained in special vessels, the latex tubules, which will be discussed later. The latex contains a large number of various compounds, e.g., sugars, starch, proteins, oils, rubber, and many other secondary plant materials (see p. 217). The milk-like appearance can be attributed to the latex being partly in solution, partly suspended as solid particles, and partly as emulsified drops.

Essential Oils

These secondary plant materials (see p. 219), which must not be confused with fatty oils, can occur in practically all plant organs. They are present in the cells as small droplets of high refractive index (Fig. 4.5A) or they may coalesce into larger drops. On dissolution of the cell wall and the protoplasts, the oil droplets of neighboring cells can coalesce, too, thus forming larger oil-storing organs (Fig. 4.5). This type of formation is known as lysigenous. These must be distinguished from

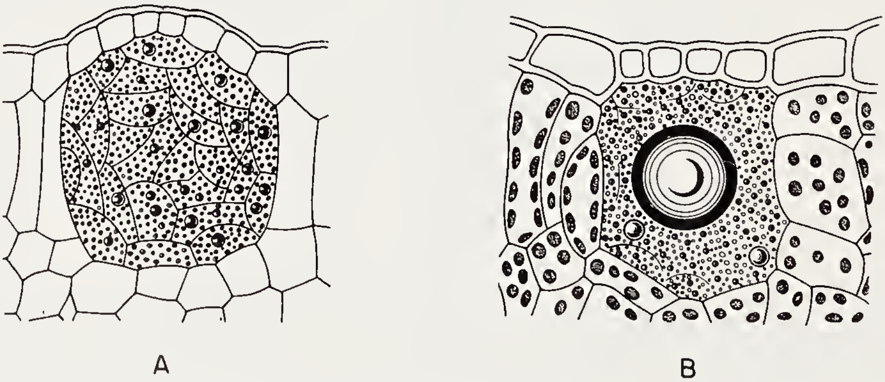

FIG. 4.5. Lysigenous formation of an oil-storing organ in the leaf of *Dictamnus albus* (dittany). (A) Before and (B) after dissolution of the cell walls; approx. 60×. (Adapted from Rothert.)

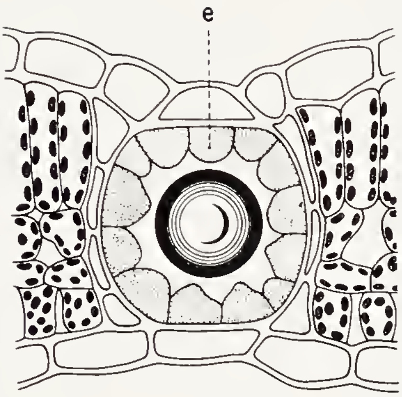

FIG. 4.6. Schizogenous oil-storing organ in the cross section of a leaf from St. John's wort (*Hypericum perforatum*). e, Glandular epithelium; approx. 80×. [Adapted from Haberlandt (1924).]

other oil-storing organs which are formed, similarly to the intercellular ones, by parting of the cells, i.e., schizogenously (Fig. 4.6). These, like the resin ducts (see p. 164) are lined with a layer of cells which keeps the oils and resins in the cavity. These cells therefore function like glands, which leads us to the later consideration of gland cells.

CHANGES IN THE CELL WALL

As has already been mentioned, the growth of the cell caused by the formation of vacuoles must bring about growth of the cell wall. Basically, a distinction must be made between growth in area and growth in thickness; the former usually precedes the latter and occurs by stretching the cell wall material and/or the intussusception of new cell wall material. The growth of the cell wall area can lead either to a general increase in cell girth (widening) or, when growth is polarized, to elongation of the cell. When the elongation is restricted to the tips of the cells the growth is described as apical; this can proceed in unipolar or bipolar fashion. The growth of embryonic cells in area is generally small, since the growth of the cell due solely to the increase in plasma material is a slow process. Only the onset of longitudinal growth, which brings about a significant and rapid increase in cell volume due to the formation of vacuoles, results in a strong plastic extension of the young cell wall; this must be compensated for by intense synthesis of cell wall material. The increase in the volume of the cell sap cavity ends finally when, due to the accumulation (apposition) of fresh cell wall layers, the cell wall becomes too rigid to allow further plastic deformation.

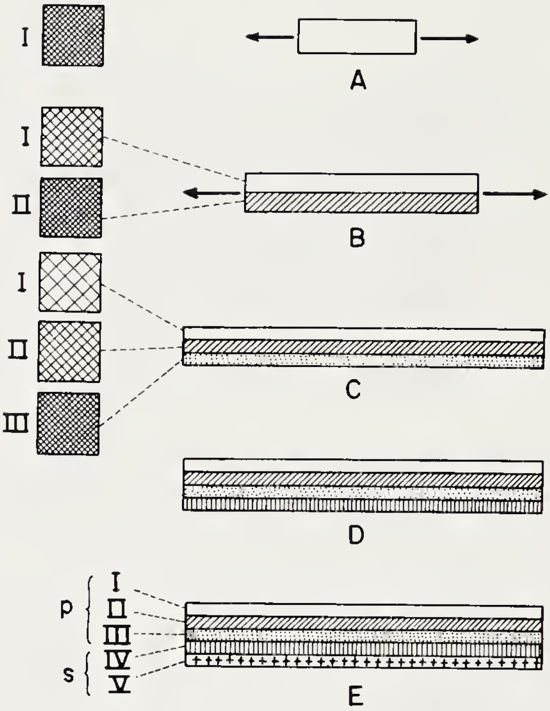

Fig. 4.7. Schematic growth of the cell wall by apposition. (A–C) Growth in area. The individual layers with the indicated mesh size are shown on the left. (C–E) Growth in thickness. The layers are numbered from I (outermost) to V (innermost). p, Primary wall layers; s, secondary wall layers.

The mesh diameter of the fibrillar network in the primary wall increases steadily in the course of the plastic extension (Fig. 4.7A–C). This would reduce the strength of the wall, but for the intussusception of new fibrils of the primary wall (Fig. 4.7B,C), which then undergo stretching themselves. The cell wall therefore maintains a constant thickness at first. This persists until the cell reaches its ultimate size. At this point the cell wall consists of many superimposed fibril networks; the mesh size increases outward (multinetwork growth). On strong longitudinal growth, the fibrils in the outer layers often appear to reorient themselves in the longitudinal direction. The end of the growth in area marks the onset of the growth in thickness, in the course of which fresh secondary wall layers are steadily accumulated by apposition (Fig. 4.7 C–E). This results in an increase of the wall thickness. Both stages of growth probably occur.

The details of the process of cell wall synthesis are still largely hypothetical. The extension of the fibrillar networks probably occurs by steady breaking and making of junctions. The polymerization of the sugar units to cellulose chains and the combination of these into microfibrils appears to occur in the tertiary lamellae. It has repeatedly been observed that the endoplasmic reticulum is strongly developed along the growing cell wall; one may therefore conclude that the sugar units are delivered to the sites of synthesis by the endoplasmic reticulum. As yet, however, nothing certain can be said about this point. The Golgi apparatus also takes part in the synthesis (see p. 41).

Apart from the overall increases in thickness, various types of local growths in thickness are also known in which the thickening is limited to certain regions of the cell wall. This leads to the formation of thickenings, networks, spines, and other formations, both on the inside and outside of the cell wall. The results of the interplay between growths in area and in thickness thus vary from case to case, so that the great variety in the shapes of plant cells is not surprising.

Secondary Alterations of the Cell Wall

Subsequent changes in the cell wall result not so much in changes in the shape of the cells but rather in the chemical and physical properties of the cell walls. This applies especially to lignification, in the course of which the already existing and thickened cell walls become reinforced by the deposition of certain compounds. On the other hand, the original character of the cell can be fundamentally altered by such depositions and accumulations as, for example, in cork tissue; this leads to the formation of a new type cell, at least in regard to cell functions. Incrustations arise when the additional materials infiltrate and impregnate already existing cell walls (Fig. 4.8A), while accretions are formed by the accumulation of additional layers (Fig. 4.8B). The chemical composition of the deposited materials is very variable.

Lignification

This occurs on deposition of certain materials known as lignins in the cellulose network, mainly in the interfibrillar spaces. Chemically, the lignins are polymers of phenylpropanes, e.g., coniferyl alcohol, cross-linked to form a three-dimensional network within the cell wall. They can be dissolved by eau de Javelle[1] or (on an industrial scale) by boiling with calcium bisulfite (sulfite liquor) which leaves only the cellulose skeleton undissolved. This procedure is used for the production of wood pulp and lignin-free paper. Lignin can be identified microscopically by a mixture of phloroglucinol and hydrochloric acid, which

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[1] Eau de Javelle contains mainly potassium hypochlorite. Its action depends on the nascent chlorine.

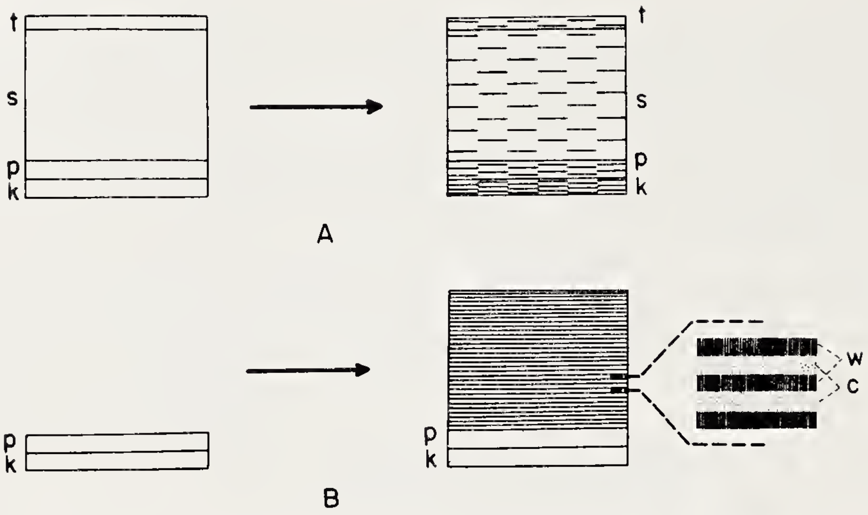
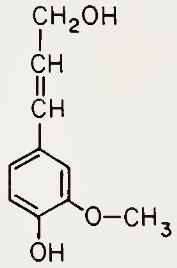


Fig. 4.8. Schematic secondary alterations in the cell wall. (A) Incrustration; (B) accretion. c, Amorphous cutin or suberin; k, connecting layer; p, primary wall; s, secondary wall; t, tertiary wall; w, monomolecular wax layer. Rod-shaped molecules in perpendicular orientation to the cutin or suberin lamellae. (After Sitte, modified.)

produces a bright red coloration. Lignification leads to an increase in the mechanical strength, especially with regard to compressive stress, but it also produces a certain loss of elasticity. The permeability of the cell walls to water is also reduced. All types of cells can be affected by lignification, but usually only secondary cell types.

Coniferyl alcohol



Apart from the lignins, tannin-type compounds are often also deposited in the cell walls. These are phenolic compounds which protect the cell walls from microbial attack. They impart a dark color to the cell walls, e.g., change from sapwood to heartwood, see p. 144.

Deposition of Minerals

Apart from organic materials, substances of inorganic nature can also be found in the cell walls of many plants. For example, calcium carbonate is deposited in the walls of numerous algae. In the alga *Acetabularia* (see p. 349) it occurs together with calcium oxalate. Silicic acid deposits are characteristic of the shells of diatoms, but they also occur in grasses, reeds, and horsetails. Such deposition always leads to a hardening of the cell walls, which lose their elasticity in the process and become brittle and fragile.

Cork Formation

This is an instance of accretion, the deposition of alternating layers of high molecular polyesters, suberin and cutin, on the one hand, and of waxes on the other (Fig. 4.8B). The waxes appear to be present in monomolecular layers, with the approximately 30 Å long, rod-shaped molecules in perpendicular orientation to the surface (Fig. 4.8B). However, the cutin and suberin are amorphous. By the accumulation of hydrophobic materials the cell wall becomes water-repellent and distinctly impermeable to water. Cell walls containing cork therefore occur frequently in inner and outer integuments where their function is to reduce or hinder the passage of water.

Suberization. In cork cells the accretion does not stop with a single suberin layer; alternating wax and suberin layers are deposited regularly in the cell wall (Fig. 4.9) in the way already described (Fig. 4.8B). The concomitant reduction in the metabolism of water and other materials finally leads to death of the protoplast. Very water impermeable layers of cells are thus produced, serving to protect the surface of a plant whose epidermis has been damaged or destroyed.

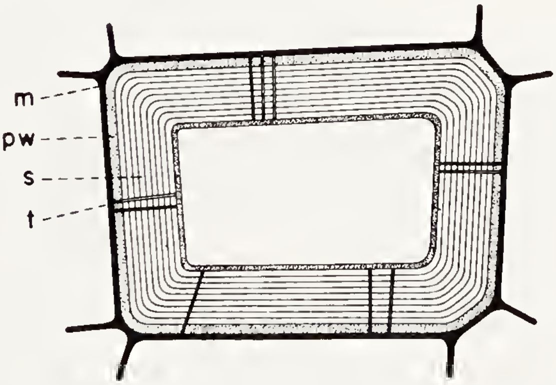


FIG. 4.9. Schematic section through a cork cell. m, Intercellular substance; pw, primary wall; s, secondary wall consisting of wax and suberin layers; t, blocked pit channels. [After Sitte (1961), modified.]

Cuticle

This is a thin continuous deposit on the external walls of epidermal cells. It appears mostly folded in cross section, the direction of the folds following the main elongation direction of the cells (Fig. 4.10). The cuticle consists mainly of cutin, secreted outward through the cell wall as a semisolid mass which then solidifies. Many plant organs, e.g., fruits (grapes, plums, etc.) and leaves (cabbage), produce a thick wax secretion which covers the surface like hoarfrost. The coating consists of rod-like or tubular wax crystals (Fig. 4.11) of various shapes. The function of the cuticle and of the wax layers apparently is to reduce the rate of transpiration. This protection against loss of vapor is improved by further cuticular impregnation of the epidermal cell walls themselves (Fig. 4.10). The intercellular cavities can also be lined with submicroscopic films of cutin.

Sporoderm

Pollen grains and spores are usually covered by a cutinized outer layer (exine) which surrounds the cellulose inner layer (intine). This protective layer often has a characteristic surface relief of warts, spikes, ridges, etc. Chemically it consists of sporopollenin, a material similar to cutin but chemically even more resistant, which remains unaltered for long periods of time. This characteristic now allows the identification of fossil pollen grains (pollen analysis).

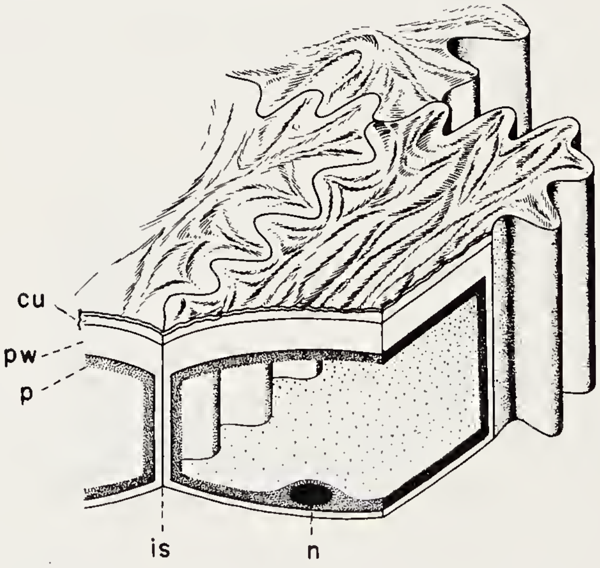


Fig. 4.10. Schematic leaf epidermis cell. The front of the cell is cut open. cu, Cuticle; is, intercellular substance; n, nucleus; p, plasma lining of the cell wall; pw, primary cell wall.

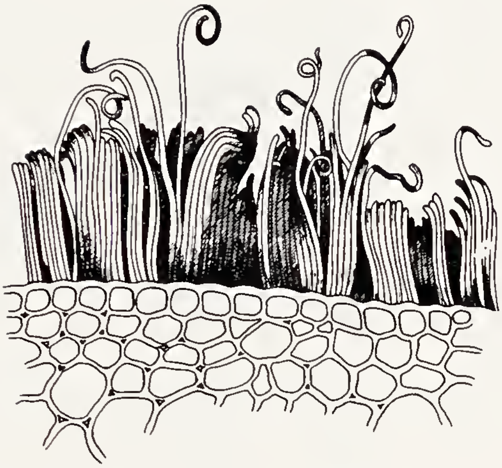


FIG. 4.11. Rod-shaped wax secretions on the stem nodes of sugar cane in cross section; approx. 150×. (After de Bary, modified.)

LOSS OF NUCLEUS

The conducting elements of the phloem, collectively called *sieve elements,* may be segregated into the less specialized *sieve cells* and the more specialized *sieve tube members.*

Sieve cells of gymnosperms and vascular cryptogams have relatively unspecialized sieve areas on both end and side walls. They are directly derived from provascular cells and do not have companion cells.

In mono- and dicotyledons, the sieve tube members are produced from the parent cells by unequal division. The larger cell develops into the enucleated sieve tube member, and the smaller, which can undergo further multiple divisions, gives rise to nucleated companion cells (Fig. 4.12). The latter plasma-rich cells, characteristic of the Angiosperms, are in contact with the plasma wall lining of the sieve tube member through numerous protoplasmic connections called *plasmodesmata.* While the sieve elements are clearly involved in the transport of organic materials, the role of the companion cells in this function is not yet quite clear, except that when the companion cell dies the associated sieve element dies also.

The obliquely set end walls of sieve cells and sieve tube members are perforated as a result of local dissolution of the cell wall. This either transforms the whole end wall into a single perforated disk (Fig. 4.12), or else end walls with several perforated regions are produced. Both sieve areas and sieve plates (sieve areas with more prominent connecting strands and callose) may occur on the side walls of sieve tube

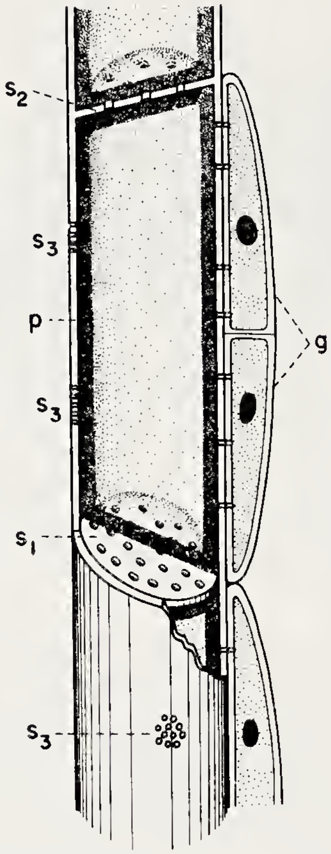


FIG. 4.12. Sieve tube members with companion cells (schematic). The upper part is dissected along the long axis. g, Companion cells; p, plasma lining wall; s, sieve plates, s_1 and s_2 in the transverse walls; s_3, sieve areas in the side walls.

members. The pores are penetrated by plasma strands and the sieve elements themselves are lined with a plasma layer; the nuclei in this layer soon perish. The lumen of the sieve elements is filled with a cell sap rich in organic materials (proteinaceous slime bodies). The sieve elements are usually active from a few weeks to a few months of one growing season. Their perforation plates are then blocked by deposits of callose (see p. 24).

LOSS OF PROTOPLAST

Sclerenchyma Cells

These are also strengthening elements, but they differ from collenchyma cells in having thick, secondary, often lignified walls and commonly lack protoplasts at maturity. Two forms of cells are distinguished, *sclereids* and fibrous forms (fibers, tracheids, vessels). The nonlignified walls are characterized by marked elasticity but become more or less rigid by lignin deposition (see p. 83). Examples are discussed below.

In summary, cells may undergo a progressive series of changes during differentiation: (1) vacuolation; (2) change in cell contents, i.e., formation of organelles or of specific cell products; (3) change in the cell wall, i.e., formation of pits and addition of wall material; (4) loss of nucleus, i.e., formation of sieve (phloem) cells; and (5) loss of protoplast. Any cell which does not differentiate beyond step three above will be a living, thin-walled *parenchyma* cell. Any cell undergoing all five stages of differentiation becomes the other mature cell type—*sclerenchyma,* e.g., xylem cells such as tracheids, vessels, and fibers.

Mature Cell Types

Plant cells may be conveniently categorized into two mature cell types—*parenchyma* and *sclerenchyma.* Any meristematic cell (undifferentiated and totipotent) which undergoes the first three stages of differentiation (vacuolation, change in cell contents, change in cell wall) is a mature *parenchyma* cell. A cell which progresses through the first four stages of differentiation (including loss of nucleus) is a special type of parenchyma, *phloem.* Any cell undergoing all five stages of differentiation (ending with loss of protoplast) is a *sclerenchyma* cell. The most important types of each are described below.

PARENCHYMA

The Isodiametric Cell

The isodiametric cell results from more or less uniform growth in area; it has approximately the same dimensions in all directions.[2] Such a cell follows the principle of the development of minimum surface area, and the shape is therefore approximately spherical, because of surface forces. The cells formed in this way are in any case not perfect spheres but polyhedrons, owing to the numerous surfaces shared with neighboring cells (cf. Fig. 4.13), and they adjust so that no intercellular spaces can be observed, as in the apical meristem.

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[2] This must not be taken too rigidly, as only a few cells would fit the description exactly. The term "isodiametric" generally describes meristematic cells and the ground tissue.

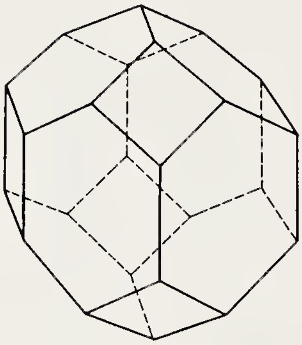

FIG. 4.13. Tetrakaidecahedron as a model of an isodiametric cell.

Parenchyma Cells

These ideally approximate the isodiametric cells although here too one dimension can be preferred, as is the case in the palisade parenchyma of foliage leaves. These living cells with their only slightly thickened, usually unlignified walls constitute the primary ground tissues of the plant body. Its turgescent tension also contributes to the plant's rigidity. The other tissues are embedded in this ground tissue, which occurs in practically all parts of higher plants. The parenchyma are rich in intercellular spaces which form a continuous aeration system. In a few cases, e.g., in aquatic plants, they can become so large that a regular aerating tissue (aerenchyma) is formed. The ground tissues can further be subdivided according to their functions. Thus, one can distinguish synthesizing, assimilating, storing, conducting, and other types of parenchyma.

Epidermis

The surface of the aerial organs of higher plants is covered with a single-layered coating or dermal tissue whose cells are joined uninterruptedly, i.e., without intercellular cavities. This tissue is known as the epidermis. The epidermal cells have characteristic shapes corresponding to their two main functions: mechanical protection of the surface, and control of the gas metabolism and the release of water vapor. These cells are mostly flat and extended, i.e., by no means isodiametric, and their side walls are often undulated (Fig. 4.10). This results in close coupling between neighboring cells and hence in increased mechanical strength. The outer primary walls of the epidermal cells are usually thickened; all other walls thicken only moderately (Fig. 4.10). Thick, even lignified, secondary walls may occur in parenchyma cells, particularly those in the secondary xylem. The outside of the epidermis is covered by a cuticle (see p. 86). Sometimes the outer walls are cutinized as well. The plasma utricle encloses a large vacuole; the cell sap in the vacuole is sometimes colored by anthocyanins. The epidermis cells often contain leucoplasts and, less frequently, chloroplasts.

Prosenchymatous Cells

Elongation of a cell in one direction gives rise to elongated cells with tapered ends. This is a result of apical or of longitudinal growth. The former is restricted to the ends of the cell, while the latter affects the middle part of the young cell as well. One-sided (unipolar) apical growth occurs in hairs, pollen tubes, and fungal hyphae and bipolar apical growth, e.g., in wood fibers. In most cases the elongated cells undergo yet another change by thickening, which can occur locally or on all sides. The functions of the resulting cells are mainly support and translocation.

Hairs

Plant hairs, also known as trichomes, arise from localized growth of individual epidermis cells. They are anchored to the epidermis at the base. A great variety of shapes and functions is encountered (Figs. 4.14, 4.15, and 4.16): they can be single- or multicelled, branched or straight, live or dead, of papillar (Fig. 3.9A) or condyle shape. Many hairs become multilayered by accumulating secondary wall layers (such as cotton wool), contain enclosures in the cell wall (see p. 92) thus altering their mechanical properties, or undergo sometimes rather complicated development corresponding to their function, such as, glandular hairs, the scalelike absorption hairs (see p. 182), or the stinging hairs (Fig. 4.15). In the latter, the lower, cyst-shaped part is embedded in a pedestal-type excrescence of epidermal and subepidermal tissue, while the top part develops into a peak and ends with a small dome. On touch this dome breaks off obliquely at a performed spot which is brittle due to embedded silica (Fig. 4.15B,C), so that a kind of hypodermic syringe is formed which penetrates the skin. The pressure exerted simultaneously on the lower part injects the cell sap, containing sodium formate, acetylcholine, and histamine into the wound.

Gland Cells

Apart from the glandular cells mentioned above (latex, oil) which deposit their secretions into the inner cavities, there are also gland cells located at the plant surfaces which dispose of their secretions externally.

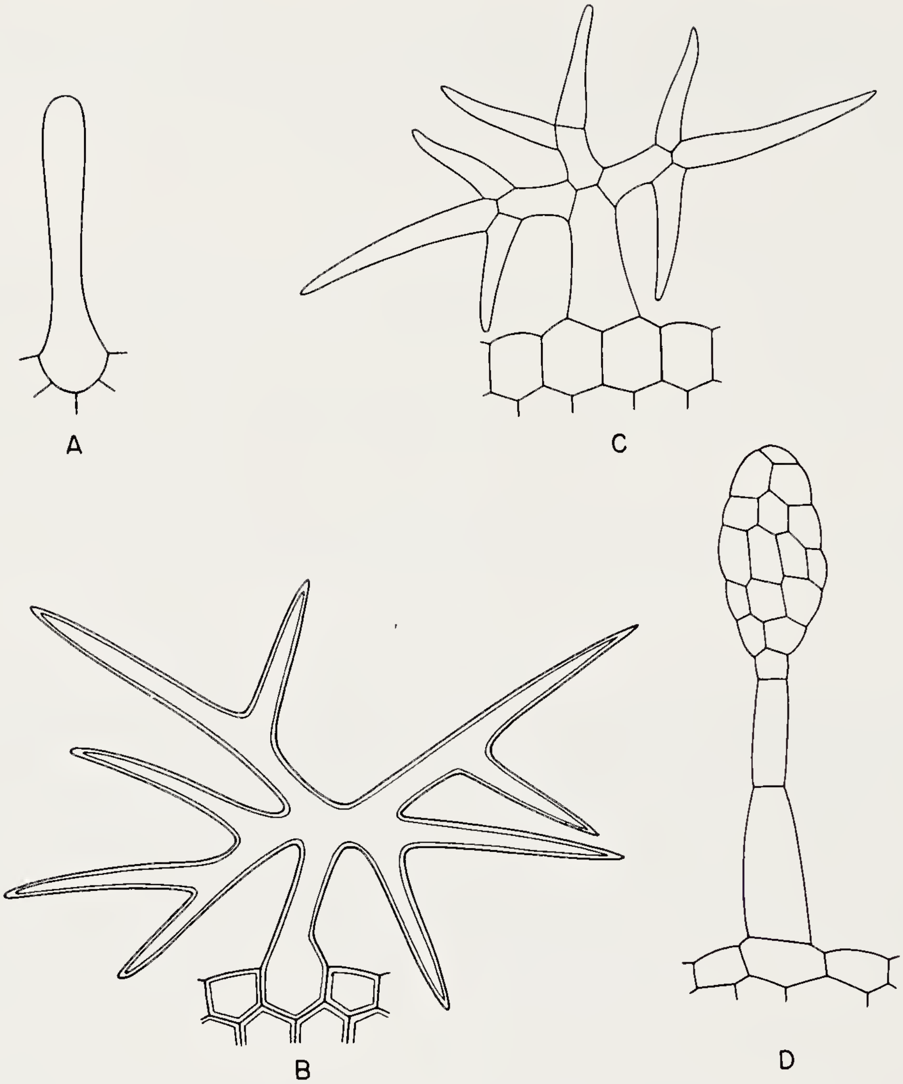

FIG. 4.14. Hair types (approx. 250×). (A) Single-celled, straight (*Fuchsia*); (B) single-celled, branched (*Matthiola incana*); (C) multicelled, branched (*Lavandula officinalis*); (D) capitate hair (*Hyoscyamus niger*). (After Troll, Hummel, and Staesche, modified.)

These can occur either singly, like the bulb-shaped glandular hairs in which the secretions are found between the cell wall and the cuticle and are released when the latter is broken (Fig. 4.16), or they can occur in groups, e.g., in the glands of insectivores (see p. 257) or in the nectar glands which secrete a sweet mucous substance or sap for attracting insects. This substance is formed in the Golgi apparatus, dispatched to the boundary layer of the cytoplasm in the sack-shaped Golgi vesicles, and is there secreted (see p. 42). Finally, mention should be made in this

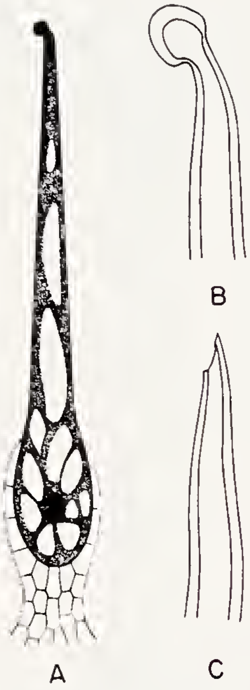

FIG. 4.15. Stinging hair of the nettle (*Urtica dioica*). (A) Hair in a pedestal in optical section (approx. 30×); (B) enlarged top; (C) broken-off top (approx. 500×). (After Kny, Kienitz-Gerloff, partly altered.)

context of the active *hydathodes,* which exude water externally in liquid form; this water frequently contains dissolved salts (guttation, see p. 187).

Collenchyma Cells

Local thickening of the primary cell walls of parenchyma cells gives rise to stiffening elements which are known as *collenchyma* cells. Angular and lamellar collenchyma can be distinguished, according to whether the thickening is restricted to the cell angles (Fig. 4.17A) or whether some of the cell walls undergo uniform thickening while others remain thin (Fig. 4.17B). The thickening consists of alternating layers of cellulose and pectin materials. Because of the presence of thin cell wall regions, the collenchyma cells are hardly hindered in their metabolism and therefore retain their plasma contents. For the same reason, they are also capable to some extent of extension and growth. They therefore occur mainly in younger plant organs which are still in the process of growing. Collenchyma cells may develop secondary walls and become lignified, thus becoming changed into fibrous sclerenchyma.

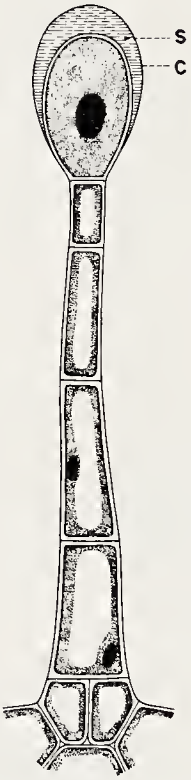

FIG. 4.16. Gland hair of sage (*Salivia pratensis*). c, Cuticle; s, secretion; approx. 300×. [Adapted from Troll (1959, p. 272).]

Laticifers

These are single cells or fused cells which contain latex and form systems that penetrate various tissues of the plant body.

Unarticulated laticiferous vessels. These unarticulated latex-containing ccnoblasts which occur, for instance, in many *Euphorbia* species (spurge) originate as single cells. The single cell develops into a tube which penetrates the plant organism as an elongated and many-branched utricle; the growth pattern follows that of the plant from the seedling stage onward. Their walls consist of layers of obliquely intersecting fibrils with a parallel texture.

Articulated latex vessels. With regard to their function and their contents, these resemble the unarticulated ones. In contrast to the latter, however, they are formed by cell fusion. Their network penetrates the entire plant organism. They occur, for instance, in the rubber tree (*Hevea brasiliensis*) and in the poppy (*Papaver somniferum*).

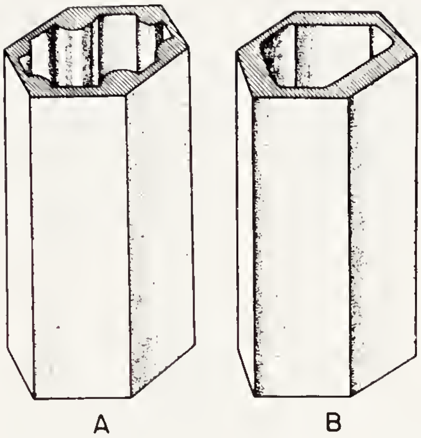

Fig. 4.17. Schematic wall thickening in collenchyma cells. (A) Angular collenchyma; (B) lamellar collenchyma.

Endodermis

This is a cell type which acts as a physiological sheath to separate the vascular tissues for the transmission of water and other materials from the ground tissues. The prismatic cells in the primary early developmental stages are in any case not fully lined; the suberinlike material (endodermin), whose chemical composition is still unknown, is deposited only in certain wall sections and runs along the four radial walls of the cell in a continuous band (Fig. 4.18A). The other parts of the cell wall remain unaffected. This band is known as the Casparian strip. Apparently its function is to prevent uncontrolled diffusion of dissolved materials through the cell walls. Later, in the secondary stage of development, the whole cell becomes lined with a layer of endodermin, while some individual endodermal cells (known as passage cells) remain unaffected. In certain cases, primarily in the monocotyledons, the radial walls contain, apart from the internal tangential walls, some accumulations of lignified cellulose layers (Fig. 4.18C); this turns them into a mechanical separating layer (tertiary endodermis). In effect, this is a thickening of the walls combined with incrustation.

SCLERENCHYMA (Sclereids, Fibers, Vessels, and Tracheids)

Sclereids are widely distributed in cortex, pith, among vascular tissues and in leaves, fruits and seeds. Foliar sclereids (idioblasts) vary from short to broad fusiform or fiberlike to irregularly or radially branched

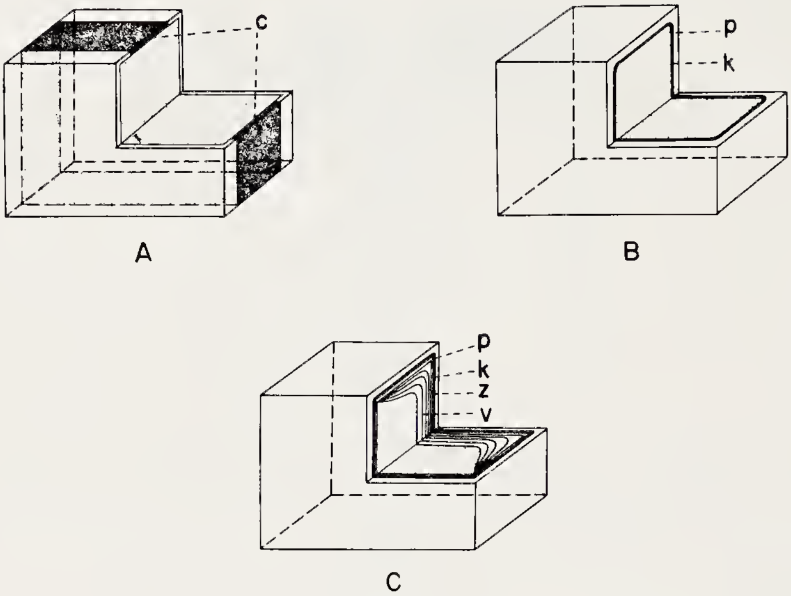

FIG. 4.18. Endodermis cells (schematic). (A) Primary; (B) secondary; (C) tertiary stage of development. c, Casparian strip; k, cork lamella; p, primary wall; v, stratified thickened layer; z, intermediate layer.

and the degree of activity of the protoplasts is variable. Thin-walled sclereids can hardly be distinguished from sclerified parenchyma. The thick-walled forms, e.g., *stone cells,* contrast with parenchyma to a striking degree.

Stone Cells

The thickening of all the walls of an isodiametric cell gives rise to so-called stone cells (sclereids). In these cells the more or less regular stratification of the strongly developed secondary wall is visible even

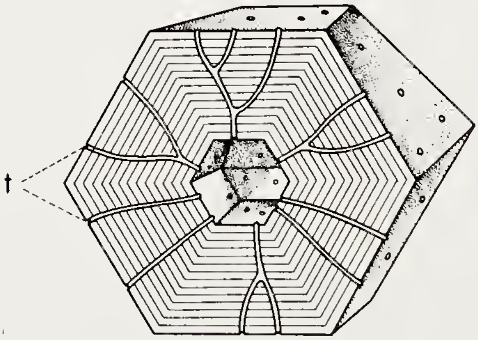

FIG. 4.19. Schematic three-dimensional diagram of a stone cell sectioned at the front. t, Pit channels.

under a light microscope (Fig. 4.19). Only the pits remain unaffected so that regular pit channels are formed. Channels of this kind may join due to continued thickening to form branched pits. The walls of the stone cells are mostly lignified (see p. 83) which increases their rigidity. They act as strengthening elements in arch structures (e.g., nutshells). The protoplast dies off after completion of the cell wall.

Fibers

The fiber cells (Fig. 4.20) are pointed at the ends and can grow to appreciable lengths, varying between a few mm and 55 cm (ramie fibers). The slitlike pits ascend diagonally in a helical pattern. The protoplast dies off on completion of the cell wall. Sclerenchyma fibers are suited to bear bending and tensile strains.

Xylem (Vascular Tissues)

Xylem is concerned with water conduction, support and storage, and may be primary or secondary in origin. Storage occurs in xylem rays and xylem parenchyma. Support is by fibers and sclereids, and also by the principal water-conducting cells: tracheid and vessel members.

Vessel members. Vessel members are formed either by complete dissolution of the end walls (simple perforation, Fig. 4.21) or by partial dissolution (scalariform perforation plate, Fig. 4.22), giving rise to perforation plates suited for the transmission of materials. It seems that only the pectinlike materials making up the matrix of the cell wall are dissolved in this perforation process. Since cellulase may be missing at this stage, the cellulose fibrils are displaced mechanically. After com-

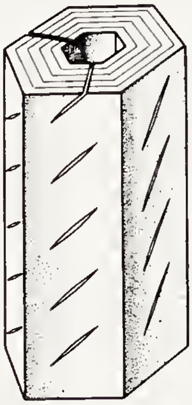

Fig. 4.20. Schematic section from a sclerenchyma fiber. The walls are regularly stratified, the slitlike simple pits run diagonally.

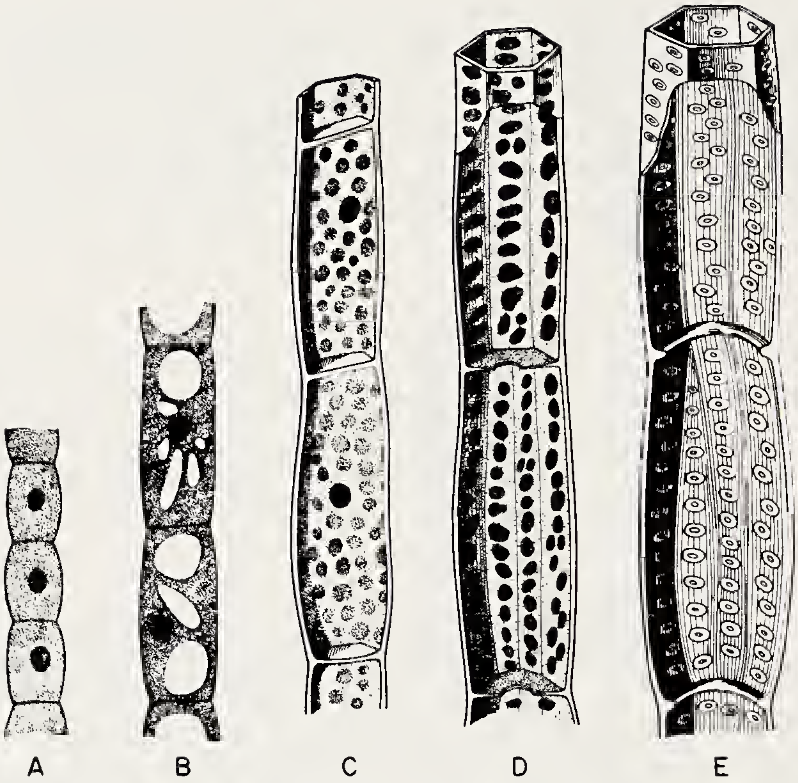

FIG. 4.21. Vessel member formation by longitudinal cell growth (A–D) and by dissolution of the end walls (D–E) to form simple perforation plates. (After Bonnier and Sablon, modified.)

pletion of the vascular tissues the protoplast dies off. Relatively long cells with wide lumens are produced in this way, which can reach lengths of a few centimeters, or in extreme cases (lianas) even a few meters. The function of these tissues is the transmission of water, which generally also contains dissolved nutrient salts. Collapse of the vessel walls due to the outward pressure of the water column rising in them is prevented by stiffening secondary wall layers. On the other hand, the possibility of exchange of water and other materials with the environment must also be preserved, so that the thickening can occur only locally. The ratio of thick and thin wall areas varies considerably. The annular vessels (Fig. 4.23A) are strengthened only by a few rings of secondary wall. The helical ones are similarly constructed, except that the thickenings are helical and run parallel to the long axis (Fig. 4.23B). In scalariform vessels the netlike thickenings cover a larger proportion of the wall (Fig. 4.23C), while the wall of the pitted vessels is practically completely thickened and only the pits remain unaffected (Fig. 4.23D). Ring and helical vessel members are found mainly in young plant organs, where they are torn up by further longitudinal growth.

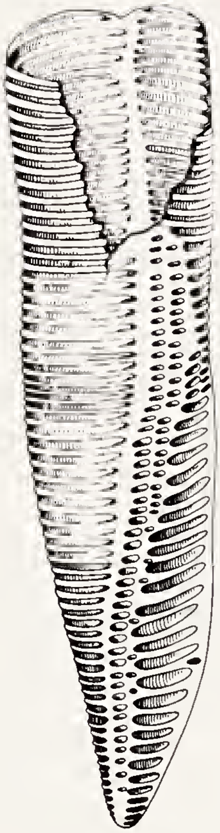

Fig. 4.22. Terminal portion of a vessel member with a scalariform perforation plate and scalariform pitting on the side walls. (After Wetzel, modified.)

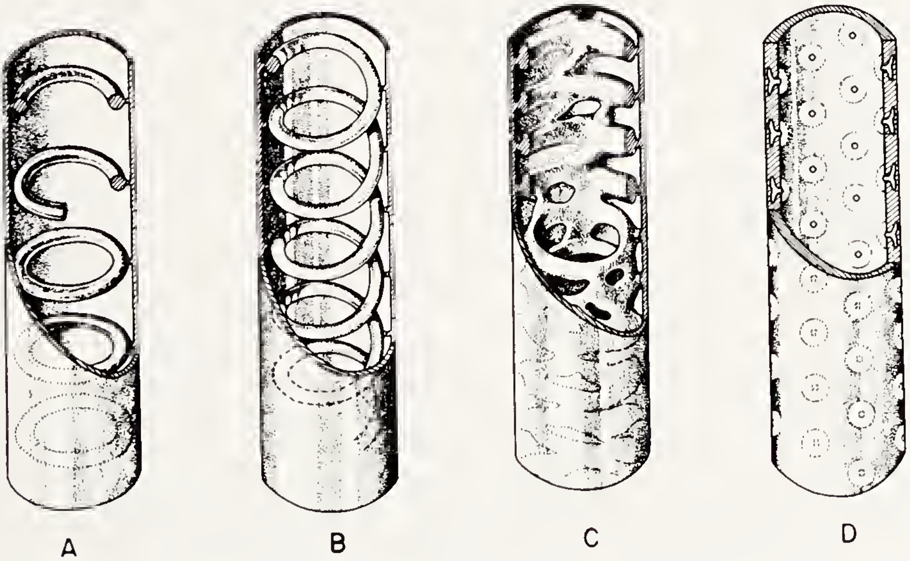

Fig. 4.23. Vessel types based upon secondary wall structure (schematic). (A) Annular; (B) helical; (C) scalariform; (D) pitted. The upper parts of all vessels are split open longitudinally.

In older plant organs their functions are taken over by scalariform and pitted vessels, together with the tracheids. The side walls of vessel elements may also be perforated, usually having *simple* (Fig. 3.16) or bordered (Fig. 3.17) pits. The tracheids exhibit the same types of wall-thickening pattern and pitting as the vessels.

Tracheids. These are elongated cells with pointed ends, suited to the transmission of water, but on marked thickening of their walls they also function as reinforcing elements (conifers, see p. 141). The cell walls are heavily pitted, accounting for the transport function of the cells. In functioning tracheids, the protoplast has already died off.

For a discussion of the origin and differentiation of *secondary* plant cell types, those derived from the vascular cambium, see Chapter 6.

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Chapter 5

Types of Organization in Plants

Some features of organization that can be regarded as characteristic of plant organisms have already been considered. At the cellular level these were the possession of a cell wall surrounding the protoplasts, the possession of organelles, and the development of vacuoles: at the molecular level, the formation of lignin, suberin, cutin, and cellulose macromolecules; the possession of chlorophyll; and the utilization of starch as a reserve substance. None of the criteria mentioned have in fact any absolute validity, as many plants have noncellulose cell walls or have no cell walls at all, have no plastids or chlorophyll, feature no vacuoles, or use some reserve material other than starch.

The same is obviously true with regard to the whole organism. Here too there are no universally valid distinctive criteria between different phyla of plants or between plants and animals. Thus, the ability for locomotion and the concomitant placement of all essential organs inside the organism to minimize the surface area is characteristic of many animals, but by no means of all; on the other hand, the sessil habit and the liberal development of surface area is not characteristic of all plants.

The distinction that the growth of animals is restricted to their youthful period, while the growth of plants extends throughout their whole lifespan and is therefore potentially unlimited, is not a universally valid distinctive criterion either. In view of all this, the classification of organisms into the vegetable and animal kingdoms can only be carried out by considering all the characteristics simultaneously. In certain cases, e.g., in the case of the flagellate algae, both green and colorless forms of which are known, we cannot make a clear distinction at all, as they can be regarded with equal justification as animals or as plants.

If we survey the vegetable kingdom, comprising about 300,000 species, we are struck by the variety of external forms with corresponding diversity of internal organization. Attempting to classify plants according to their degree of external and internal differentiation, we obtain a gradation of organized forms that extends from the relatively simple[1] unicellular organisms to the multicellular, highly differentiated bodies of the higher plants.

To a certain extent this hierarchy of forms of organization reflects the phylogeny of the plant kingdom, which certainly started with unicellular organisms. The details of the transition from the coacervate to the cellular stage, and the exact moment in evolution from which living organisms can be said to date is still unknown. Nor do we know what the first primeval unicellular organism looked like—whether it was similar to those existing today, such as bacteria or flagellates, or whether these have developed from a common precursor. It is, however, rather likely that the first live organisms were heterotrophic and fed on the organic materials in the primeval sea while the autotrophic organisms adapted to chemosynthesis (see p. 215) and photosynthesis (see p. 200) developed only later when the nutrient reservoir of the primeval sea became very depleted.

Evolution could have progressed via loose cell aggregates and cell colonies toward true multicellular organisms whose cells were already differentiated sufficiently for a distribution of functions. This type, still suited to aquatic life, is comparable in its organizational state to the present-day thallophytes. The transition to life on land necessitated further differentiation which ended with the body of the higher plant divided into shoot, leaf, and root.

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[1] The term "primitive," often used in this context and implying a negative evaluation, seems rather inappropriate for these organisms. The construction of a universal cell exhibiting all functions simultaneously must be more complex, and must therefore represent a higher state of organization from the cell physiological point of view than the construction of a differentiated cell with limited functions.

Protophytes

The simplest developmental stage, at which the individual cell is equivalent to a whole organism, is described by the term protophyte. It must, however, be emphasized that this concept defines only a form of organization and not a group in the natural system of plants. This is already evident from the fact that many taxonomically very different groups (see p. 400), such as all bacteria and Cyanophyceae, many algae, and some lower fungi, are protophytes. The daughter cells produced on division are, in any case, often held together for a while by mucous capsules or sheaths. This gives rise to the so-called cenobia (Fig. 5.1A) or even thread-shaped groups of cells (Figs. 5.1G, 5.4A) which are loose groups of cells and cannot be regarded as higher developmental stages since the single cells are also capable of individual existence. Cell aggregates consisting of motile, membrane-covered cells which fuse to form a multicellular mass are known as *plasmodia.*

Organization of the individual species differs considerably even at the unicellular level. There are two particular characteristics which serve to distinguish two main groups. The first group (eukaryons) including bacteria and the Cyanophyceae, is characterized by the lack of a true nucleus and the lack of plastids (see p. 46), while members of the other group (karyons) always contain both a nucleus and (insofar as they are autotrophic) plastids.

THE BACTERIAL CELL

When bacterial cells a few microns in diameter are said to have no nuclei, this only means that they do not possess a true nucleus with the characteristics that have been described as typical. Deoxyribonucleic acid could easily be identified in all bacteria analyzed for this purpose. However, it is not bound to basic proteins like chromosomal DNA, but occurs mainly in distinct round, oval, or irregular and diffuse regions which are described as nuclear equivalents. These correspond to the nucleus functionally as genetic control centers, but they differ in not having a nuclear membrane. The division of nuclear equivalents which regularly precedes the division of bacterial cells is also different from mitosis and its mechanism of chromosome division. It is, however, known from genetic experiments that the genes in the nuclear equivalents are also arranged linearly (they are therefore known as lineomes), and that

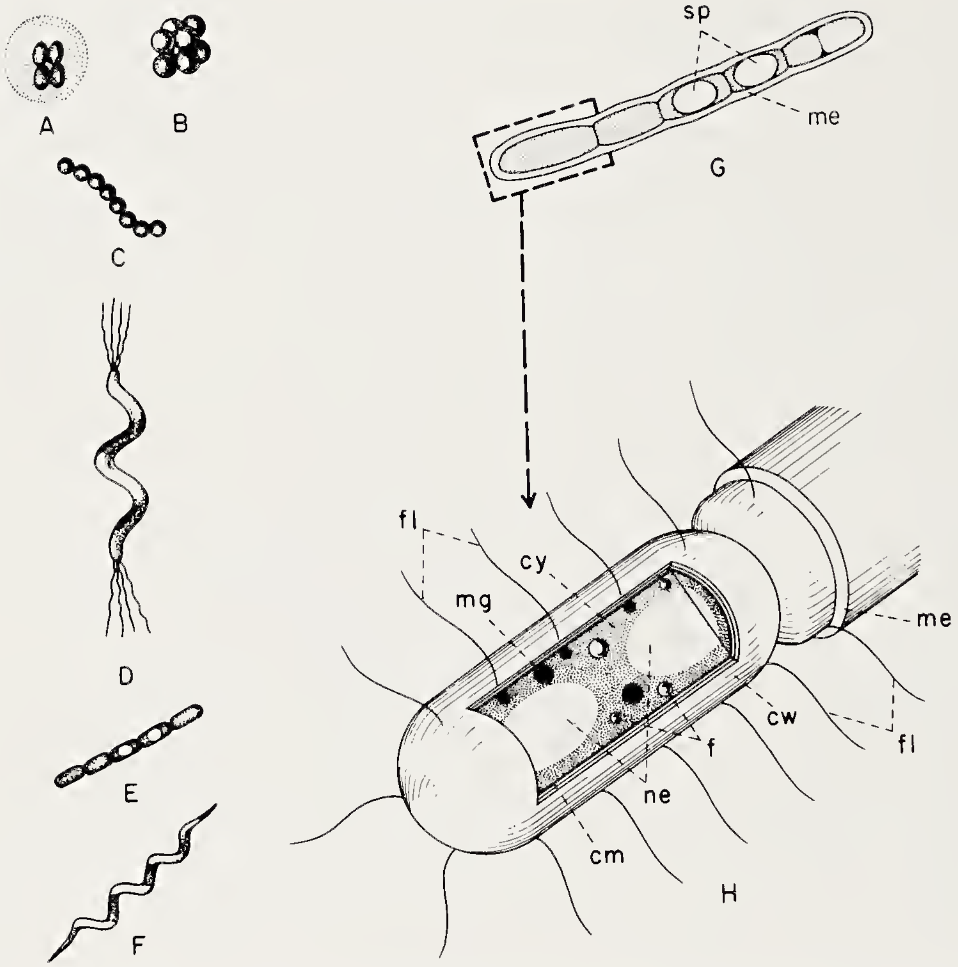
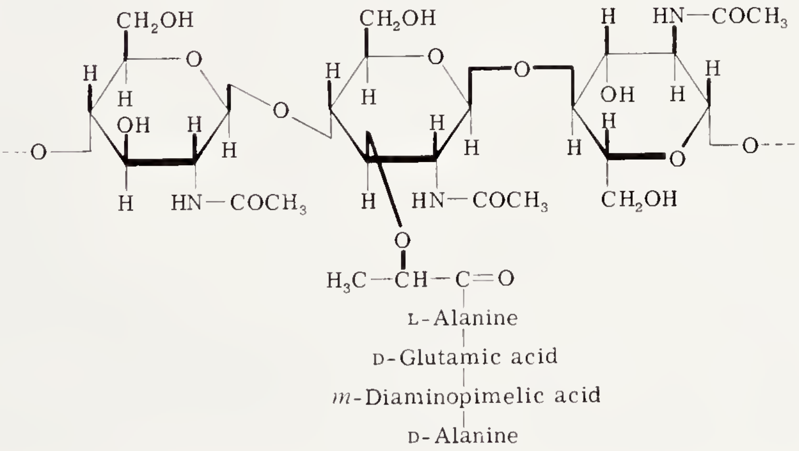


FIG. 5.1. Bacterial cells. (A) *Gaffkya tetragena,* in mucous capsules; (B) *Sarcina;* (C) *Streptococcus;* (D) *Spirillum;* (E) *Bacillus;* (F) *Treptonema* (spirochaete); (G) *Bacillus megaterium* as seen under a light microscope (approx. 1500×). Cells surrounded by a mucous envelope, two cells with spores, one cell in the process of division; (H) schematic diagram of G after electron micrographs. Mucous envelope partly removed, cell cut open. cm, Cytoplasm membrane; f, strongly refracting droplets (fats); fl, flagella with basal corpuscles arranged peritrichally; mg, metachromatic granule; ne, nuclear equivalent; cy, cytoplasm; me, mucous envelope; sp, spores; and cw, cell wall.

on division, the duplicates are divided equally between the two daughter cells (see p. 296) as is known to be the case for chromosomes. In the electron microscope (Figs. 5.1H, 5.2A) the nuclear equivalents appear somewhat poorer in contrast (light zones) than the cytoplasm which scatters electrons more strongly. As is apparent from Fig. 5.2A, they are filled with DNA structures, although the views on the structural details of the bacterial lineome are still diverse. In *Escherichia coli* each nuclear equivalent contains only one lineome in the shape of an unbranched, ring-shaped double DNA strand closed upon itself. Since, according to recent estimates, the length of this DNA is about 1 mm, while the length of the bacterial cell is about 2 μ, it must be tightly wound and coiled within the cell.

The cytoplasm has an outer boundary layer known as the cytoplasmic membrane (Figs. 5.1H, 5.2A). Structurally, this is built up of lipoproteins and corresponds to a unit membrane. Its function, similar to the plasmalemma in plant cells, is that of a physiological barrier controlling the entry and exit of materials. It is, moreover, a carrier of many enzymes, especially respiratory ones, and as such it fulfills the function of mitochondria. Whether mitochondria occur, too, is as yet uncertain. Although tubular organelles (Fig. 5.2B) have in fact been found in some bacteria, the views on their functions are still conflicting. Among the granules occurring in the cells of many bacteria, the ones so far best investigated are the metachromatic granules, formerly known also as volutin grains. These are rich in polyphosphates, i.e., condensed chain phosphates, which apparently serve both as energy carriers and as phosphate reserves. They can also contain ribonucleotides. The latter are also found in the ribosomes. Other granules consist of lipids, poly-β-hydroxybutyric acid, polysaccharides (glycogen), and, in the sulfur bacteria, polysulfides.



Section from a muropeptide (*E. coli*)

The cell wall of bacteria, 100–400 Å thick, differs fundamentally both in its fine structure and its chemical composition from the cellulose walls of plant cells. Fibrillar structures have so far never been observed. The best known at present is the multilayered cell wall of the gram-negative bacteria. The innermost layer, which determines the form and stability of the cell wall, consists of murein, which is built of muropeptides. The latter consist of the amino sugars acetylmuramic acid and acetylglucosamine which are arranged in an alternating sequence

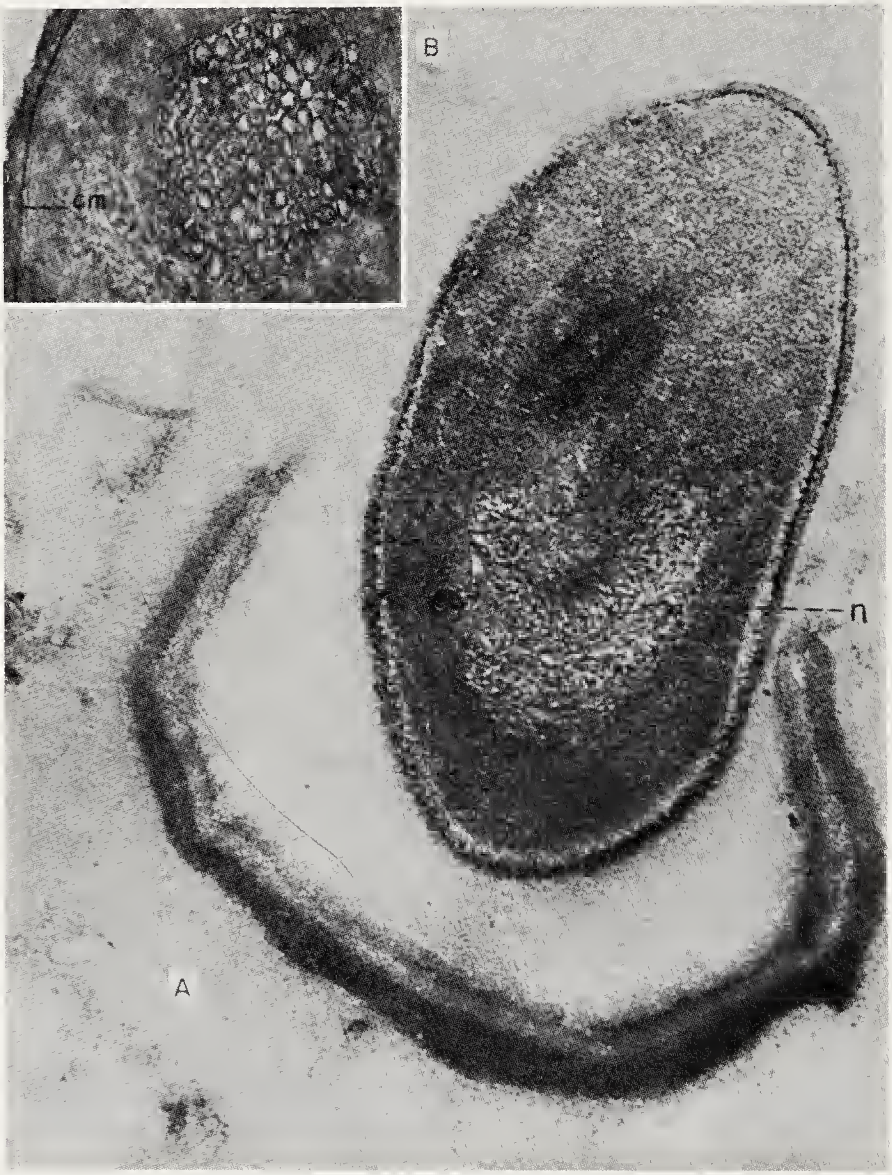


FIG. 5.2. *Bacillus megaterium.* (A) Electron micrograph of an ultrathin section through a germinating spore; 110,000×. cm, Cytoplasm membrane; n, nuclear equivalent with DNA structures. (B) Mitochondrion equivalent with tubular inner structure; the tubuli are obliquely sectioned; 130,000×. The cell wall is thicker here, in a vegetative condition, than that of the germinating spore. (Original photographs by Dr. P. Giesbrecht.)

in chains. The acetylmuramic acid carries shorter peptide side chains, which, apart from *meso*-2,6-diaminopimelic acid and L-alanine also contain D-amino acids such as D-glutamic acid and D-alanine (cf. above, the muropeptide of *Escherichia coli*). The muropeptide chains are cross-linked through peptide linkages and so murein can to a certain extent be regarded as a single, bag-shaped giant molecule which encloses the cytoplasm of the bacterial cell. Proteins, polysaccharides, and lipids are deposited on the murein in the form of lipoproteins and lipopolysaccharides; the latter determine not only the serological behavior but also the function as endotoxins (bacterial pyrogens). Muropeptides are also found in the cell walls of gram positive bacteria, but it is not yet certain whether they occur in the same arrangement as in the gram-negative ones. Moreover, these cell walls contain further components which do not occur in the gram-negative bacteria; these account for their response to gram staining.[2] The gram response is species-specific, apart from a few gram-labile forms, and has diagnostic value in bacteriology. In many cells the walls are covered with mucous envelopes (Fig. 5.1) which contain polysaccharides and sometimes also polypeptides. They form either ill-defined mucous areas or sharply defined capsules of higher viscosity.

Since some bacteria, e.g., the so-called purple bacteria, are suited to photosynthesis as well, the question of the presence of chromatophores arises. It has been assumed for a long time that the pigments (bacterial chlorophyll, carotenoids) are diffusely distributed in the plasma, but recently lamellar lipoprotein structures were discovered which carry the pigments as monomolecular layers. They can be stacked in packets or be of vesicular or other shape (Fig. 5.3), and should be regarded as thylacoids existing free in the plasma and not separated from it by a special membrane like chloroplasts. They are formed by pinching-off from the cytoplasmic membrane.

Many bacteria are provided with flagellae arranged either singly or in groups at the ends of the cell or distributed peritrichally all over the cell surface (Fig. 5.1H). Tufts consisting of many flagellae are also common (lophotrichous arrangement) (Fig. 5.1D). The flagellae originate from thickened basal granules located in the cytoplasm (Fig. 5.1H).

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[2] In gram staining the bacteria are stained with certain aniline dyes (phenol gentian violet, crystal violet, or others) followed by treatment with a solution of iodine in aqueous potassium iodide. On certain bacteria, i.e., the gram-positive ones, the dye is so strongly adsorbed that it cannot be removed by washing with alcohol, while gram-negative bacteria are rendered colorless again by such treatment.

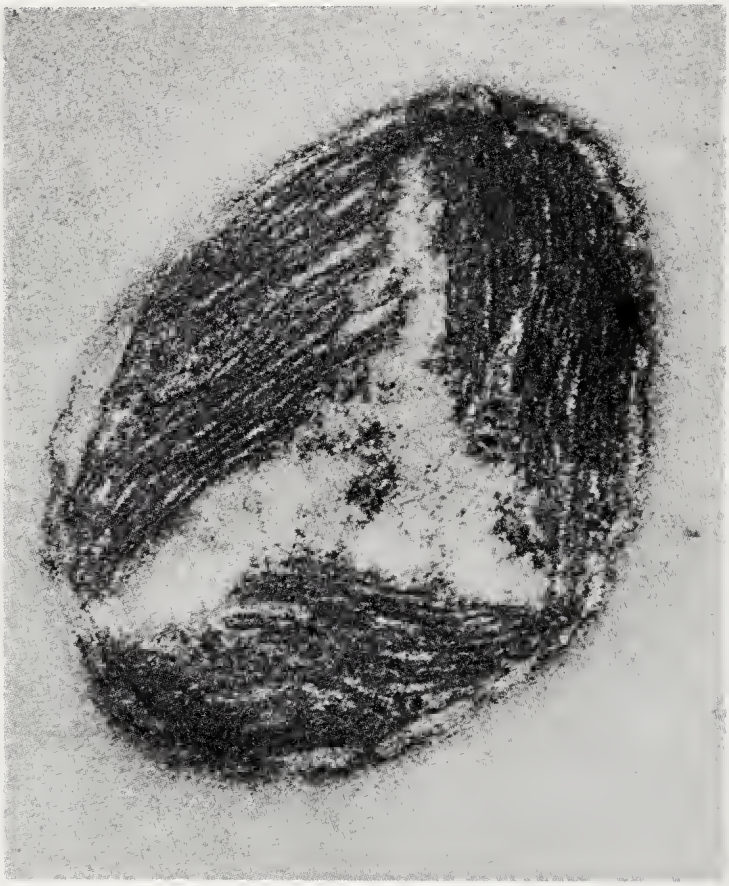

Fig. 5.3. *Rhodospirillum molischianum.* Electron micrograph of an ultrathin section. The thylacoids are arranged in three stacks; 100,000×. (Original photograph by Dr. P. Giesbrecht and Prof. G. Drews.)

The Cell of the Cyanophyceae

The above description of the bacterial cells applies to a certain extent to the cells of the Cyanophyceae (blue-green algae) which occur as single cells, cenobia, or in threads (Fig. 5.4A). These too are characterized by the absence of a true nucleus. Certain regions of the centroplasm must be regarded here as nuclear equivalents, which contain rodlike or thread-shaped DNA elements (Fig. 5.4B). Although it must be assumed that a regular distribution of the previously duplicated DNA occurs between the daughter cells in every cell division, there have so far been no observations of mitosis-type phenomena, so that the mechanism of the division of DNA is still unclear, just as in bacteria.

The Cyanophyceae are autotrophic, and yet they do not possess plastids. The pigments of photosynthesis (chlorophyll a, carotenoids,

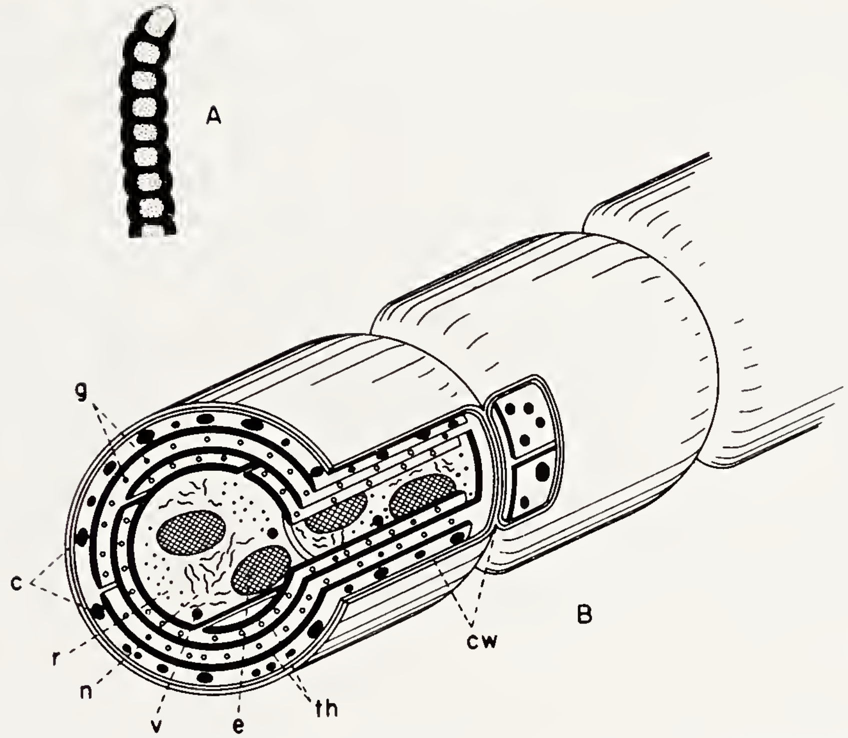

Fig. 5.4. *Oscillatoria chalybea* (Cyanophyceae). (A) In the light microscope (approx. 1500×); (B) schematic diagram, after electron micrographs, c, Cyanophycine grains; e, endoplasts; g, interlamellar granule; th, thylacoids; n, DNA elements; r, ribosomes; v, volutin granules; and cw, cell wall.

phycocyanin, phycoerythrin) are located on thylacoids which, just like those in the purple bacteria, are not separated from the cytoplasm by a special membrane. They are usually found in the peripheral areas of the cell (chromatoplasm) more or less distinct from the colorless centroplasm (Fig. 5.4A,B). Sometimes they run parallel to the cell wall (Fig. 5.4B), but in other species their course can be irregular, e.g., undulating or even radial, as generally there are great differences in the internal composition of the various species. The scheme in Fig. 5.4B must therefore be regarded only as a particular type chosen from a wide variety of types.

The protoplast, too, differs from that of a typical plant cell. It is gel-like, has no vacuoles containing cell sap, and shows no plasma currents, (see p. 75). Among the granular inclusions, some of which are certainly reserve substances, cyanophycin granules and the volutin granules have been identified with certainty; the former consist of glycoproteins, and are mostly located peripherally, while the latter consist of polyphosphates (Fig. 5.4B). Ribosomes too have been identified in the centroplasm. Apparently there are still other as yet chemically uncharacterized granular inclusions, e.g., the so-called endoplasts in the centroplasm and the 200–400Å granules, often arranged in chains between the lamellae of the chromatoplasm. Special enzyme-active regions have also been found, which may be regarded as mitochondrial equivalents. The cell wall has two layers along the side walls and three along the transverse walls (Fig. 5.4B). Externally it can be covered with a mucous envelope, which itself appears to be stratified. Which of these layers can be regarded as belonging to the cell wall proper cannot be ascertained. The innermost layer of the cell wall, in direct contact with the plasma, consists of the same amino acids and amino sugars as the muropolymer supporting membranes of gram-negative bacteria, although the components occur in somewhat different proportions. Together with the absence of a true nucleus, this fact indicates that the bacteria and the Cyanophyceae are descended from common ancestors and form an independent branch of the phylogenetic tree.

Flagellates

The group of flagellates whose members are characterized by having at least one flagellum (Fig. 5.5) includes colorless, heterotrophic, and colored, i.e., autotrophic forms. The origin of the higher algae can be

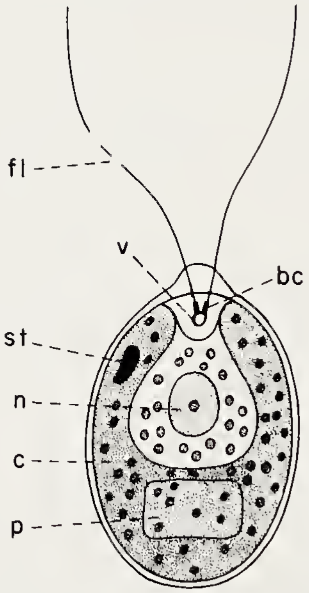

Fig. 5.5. *Chlamydomonas angulosa* (approx. 1500×). st, Stigma; bc, basal corpuscle; c, watchglass-shaped chromatophore; fl, flagellum; n, nucleus; p, pyrenoid; and v, vacuoles. [After Dill, from Oltmanns (1922, p. 205), modified.]

traced back to flagellates, as shown by the sexual (gametes) and asexual (zoospores) swarm cells in many groups; they, or rather their ancestors, are therefore regarded as the prototypes of the primeval unicellular organisms.

The flagellates differ from both of the groups discussed above in that they possess a typically organized nucleus (Fig. 5.5) together with the rest of the plasma structures and organelles characteristic of eukaryons, such as dictyosomes, endoplasmic reticulum, mitochondria, and chromatophores (see Figs. 3.3, 3.4, and 3.8). The flagellae originate from basal corpuscles located in the plasma. In typical cases, the cells contain an eye spot (stigma, Fig. 5.5), located near the base of the flagellum and colored red by carotenoids; this is produced by conversion from a chromatophore or from a part of one. Its function will be discussed later (see p. 390). Contractile vacuoles can also be found in many cases.

The flagellate cells are not naked protoplasm and cannot move about ameboid fashion, as in the less organized plasmodia; the cell wall contains cellulose, in addition to pectins. Cellulose is the typical plant cell wall material, and starch as well as oils and the polysaccharide leucosine appear among the assimilation products (see pp. 22–24).

OTHER UNICELLULAR ORGANISMS

As has already been mentioned, unicellular organisms occur in many groups of algae, e.g., in the Chlorophyceae (green algae), the Chrysophyceae, Xanthophyceae, the Diatomeae (siliceous algae), Rhodophyceae (red algae), and also in the lower forms of Phycomycetes (algal fungi). This is a further argument for the view that all algal species, and some of the fungi, too, have developed from protophytic ancestors. Since representative members from each group cannot be discussed for reasons of space, the spherical green alga *Chlorella vulgaris* (Fig. 5.6)

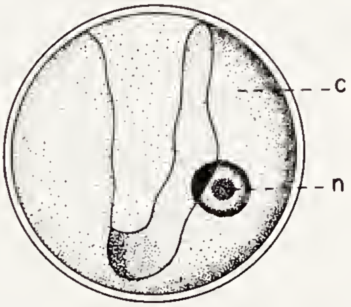

FIG. 5.6. *Chlorella vulgaris* (Chlorophyceae) (approx. 1500×). c, Chloroplast; n, nucleus. [After Grintzesco, from Troll (1959, p. 167), modified.]

can be considered as typical of the unicellular organisms without flagellae. The nucleus is covered by a pure green, watchglass-shaped chloroplast, which contains chlorophyll a and b in addition to carotenoids. The reserve material is starch, and the cell wall consists mainly of cellulose.

Cell Colonies

The typical cell colony, which can here be represented by *Pandorina morum* (Fig. 5.7), consists of a large number of undifferentiated and therefore mutually equivalent cells which have been produced from each other by division. They are therefore grown together congenitally and not postgenitally like the cell aggregates. In many forms the cells are connected by plasmodesmata and can therefore function as a physiological unit; this distinguishes them from the simple cell aggregates. In *Pandorina,* 16 *Chlamydomonas*-like cells with two flagellae each are united to form a colony covered externally by a gelatinous envelope. The universality of these cells is due to the fact that each cell is also suited for individual existence after leaving the colony.

Apart from these uniform relatively simple colonies, highly developed forms are also known, which must be regarded as true multicellular organisms. *Volvox* (Fig. 5.8) can be given as an example. In many species the cells can number up to 10,000 per organism; they are embedded in a gel-like mass (Fig. 5.8B) which forms a hollow sphere (Fig. 5.8A). The flagellae are directed outward. The cells are in contact by means of plasmadesmata (Fig. 5.8B), and this turns the sphere into an organism functioning as a unit. It is built in a polar manner. The organism moves with the vegetative region in front; the stigmae in this region are larger than in the reproductive region at the opposite pole.

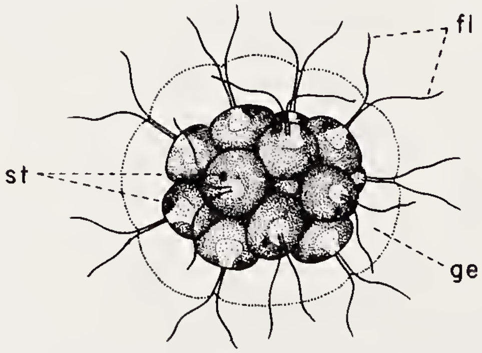

Fig. 5.7. *Pandorina morum,* a 16-cell colony (approx. 500×). st, Stigma; fl, flagellum; ge, gelatinous envelope. (After Smith, modified.)

This is where the reproductive cells are formed; these are much larger than the vegetative ones, which serve in nutrient uptake and locomotion (Fig. 5.8A). The vegetative cells die after fertilization. In contrast to the potential immortality of the protophytes, these organisms

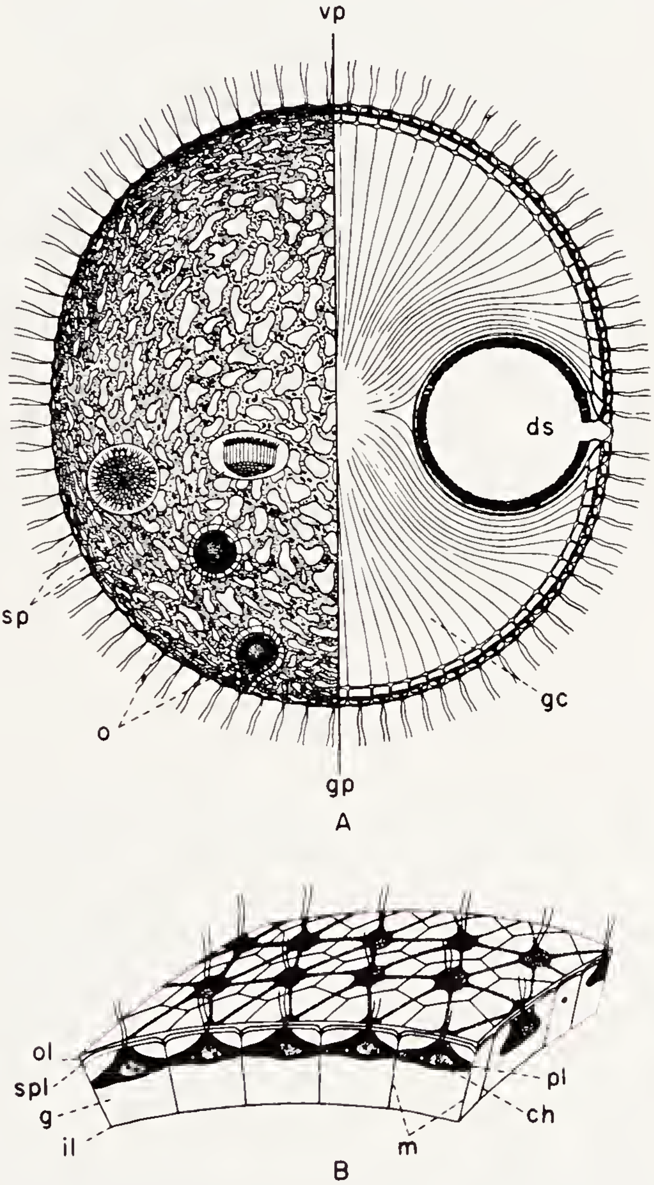

Fig. 5.8. *Volvox globator.* (A) Sphere, left in face view right in cross section (approx. 70×). (B) Schematic section of sphere, higher magnification. ol, Outer layer; spl, special layer; ch, chloroplasts; g, jelly; gp, generative pole; gc, gelatinous cylinder; il, inner layer; m, central lamella; o, oogonium; pl, plasma; sp, spermatozoids; ds, daughter sphere; vp, vegetative pole. [(A) is modified after Cohn and Janet, from Oltmanns.]

are mortal; this, together with a differentiation for the division of functions into vegetative and reproductive cells and the development of polarity is a criterion of a true multicellular organism, which can no longer be regarded as a cell colony.

CENOBLASTS

Even among the group of protophytes there are members which possess many nuclei during the main phase of their development and therefore do not strictly fall under the definition of a cell given above. In some organisms, e.g., in many Siphonales and Phycomycetes, this trend leads to the development of formations much larger than the average cell and usually of tubular shape. These contain a great number of nuclei, and are therefore multinucleated (Fig. 5.9). For reasons already mentioned (see p. 55) these can no longer be regarded as cells; they are known as cenoblasts. In the group of Phycomycetes, an example of which is the mold *Mucor mucedo,* the cenoblasts form tubelets, here known as hyphae or threads; these hyphae form an extensive multiple-branched plexus or *mycelium* (Fig. 5.9A), with numerous nuclei and no transverse dividing walls.

Thallophytes

In contrast to the protophytic form of organization, the thallus is a multicellular and sometimes also multinuclear structure. In the typical case it is adapted to aquatic life. Its cells are often already differentiated for a variety of functions. Its history of evolution can be traced back to the protophytes, to which it is connected by transitional forms such as cell aggregates, cell colonies, and cenoblasts, which have already been discussed in the previous section.

THREAD-TYPE THALLUS

Thread-type cenoblasts are produced by one-dimensional growth of an embryonic cell combined with numerous nuclear divisions; a thread-type thallus, on the other hand, can easily be derived from a unicellular organism. In the simplest case, it consists of a row of mononuclear cells. A very instructive example is the green alga *Ulothrix zonata* (Fig. 5.10). Its threads which are anchored with a rhizoid cell (Fig. 5.10A) emit

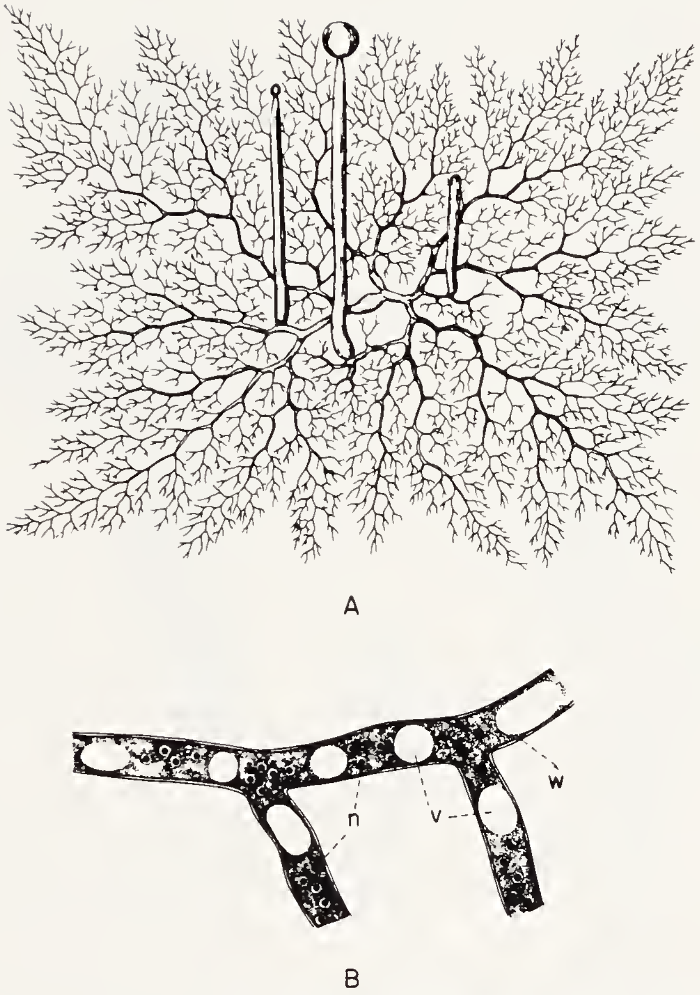

FIG. 5.9. *Mucor mucedo* (Phycomycetes). (A) Mycelium (approx. 50×) with sphorophylls; (B) single hyphae (approx. 500×). n, Nuclei; v, vacuoles; w, cell wall. [(A) after Kny (1879).]

bundles of four flagellae (Fig. 5.10B) which anchor themselves at their flagellar end (Fig. 5.10C). This cell gives rise to a new thread or filament by numerous divisions perpendicular to the long axis (Fig. 5.10D). Each cell in the thread retains its capacity for division (except for the rhizoid cell, the chromatophore of which dies); the growth is therefore intercalary. Each cell in the thread is fundamentally able to produce zoospores and gametes (see p. 270), so that the cells are therefore mutually equivalent.

The predominantly sessile (localized) way of life of the thread-type algae soon gave rise to pronounced polarity, which manifests itself first of all in the formation of an apical cell. This is the only cell capable of division, and divides itself diagonally to the long axis of the thread by

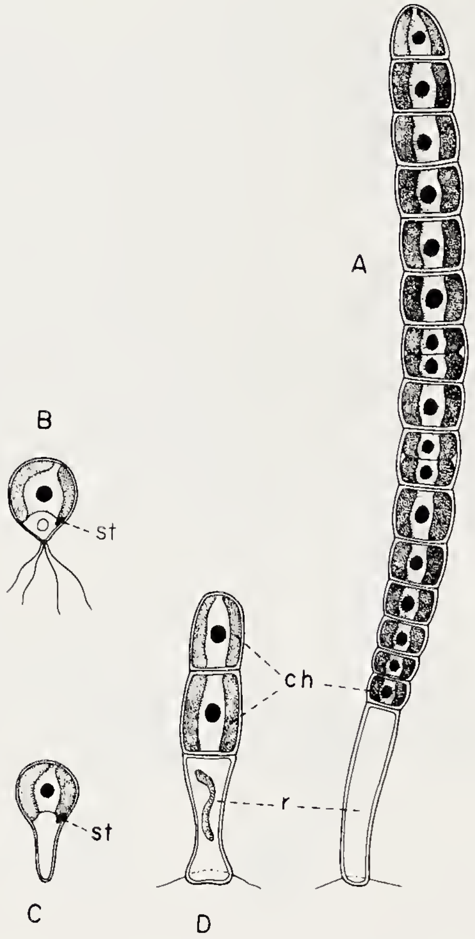

Fig. 5.10. *Ulothrix zonata* (Chlorophyceae). (A) Thread-type thallus, with anchored rhizoid cell (approx. 500×); (B) zoospore with four flagellae (approx. 750×); (C) zoospore in the process of attaching itself (approx. 750×); (D) young, fully grown thread (approx. 750×). st, Stigma; ch, chloroplasts; r, rhizoid cell. (After Dodel, Klebs, West, and Stocker, partly modified.)

steadily producing fresh segments at its base (Fig. 5.11C). It is therefore cut up in one plane. There are also transitional forms, capable of both apical and intercalary divisions.

The development of the apical cell is accompanied by branching of the threads. This imparts a bushy appearance to the thalli, as in the widespread green alga *Cladophora* (Fig. 5.11A,B). The segments produced by the apical cell in this alga are polynuclear (see p. 55). The side branches are produced either by the formation of new apical cells from lateral oblique cut outs from older cells of the thread (Fig. 5.11C) or by the apical cell itself which undergoes division sideways.

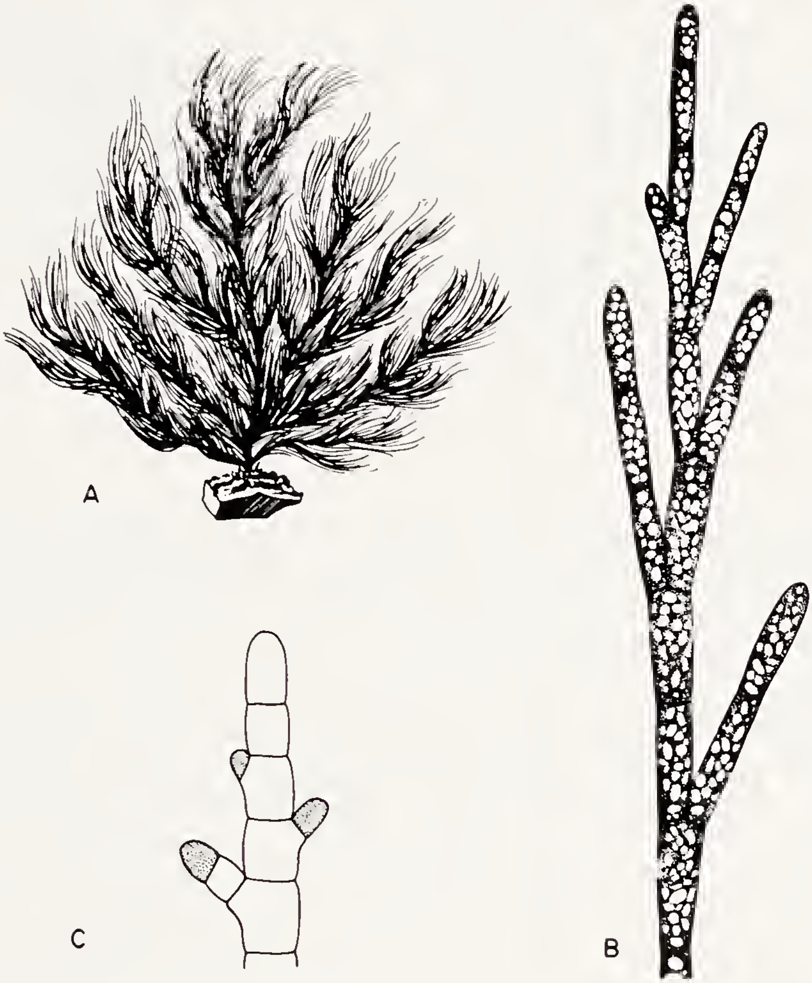

FIG. 5.11. *Cladophora* sp. (Chlorophyceae). (A) General view (approx. to scale); (B) branched thallus (approx. 50×); (C) schematic growth of apical cells and branching. [(C) after Stocker (1952, p. 49), modified.]

Further examples of single-row, side-branched filiform thalli are the colorless hyphae of Ascomycetes and Basidiomycetes, the cells of which have one or two nuclei (Fig. 5.12A,C).

LICHEN THALLUS

The more highly developed types of thalli can be traced back to the thread-type thallus. The relationships are especially clear in the case of the so-called lichen thalli, which occur in many higher algae (primarily in the red algae Rhodophyceae), but they also appear in the shapes of the compound sporophores of fungi. The thalli of the red alga *Furcel-*

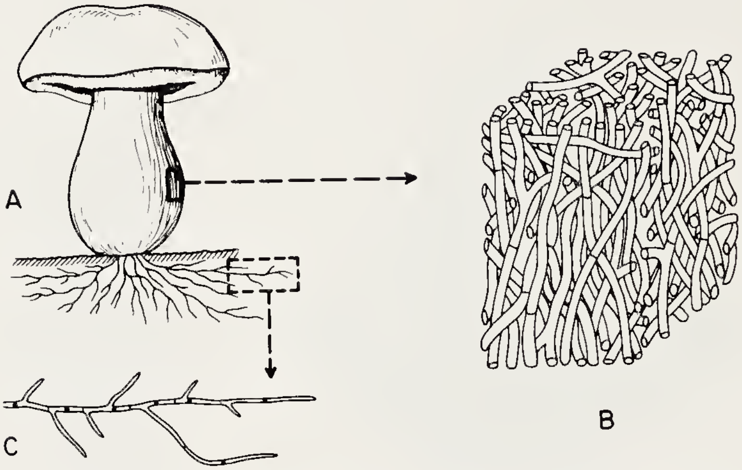

FIG. 5.12. *Boletus edulis* (Basidiomycetes). (A) Mycelium with sporophores (scale approx. 1:4); (B) perspective view of mycelium from the stem of the fruiting body (sporophore) (approx. 150×). For the sake of clarity the connections of the cross-link binucleate mycelium (cf. p. 285) are not shown; (C) hyphae from a haploid mycelium (approx. 70×).

laria fastigiata are more than 10 cm long, round, of cartilaginous feel, and are anchored to stones with clawlike rhizoids (Fig. 5.13A). The central core of these algae consists of threads arranged in parallel which are branched laterally like a fountain. The outermost cells of these branches join up to form a firm cortical layer (Fig. 5.13B). In other species the branches can originate from a single central thread. The

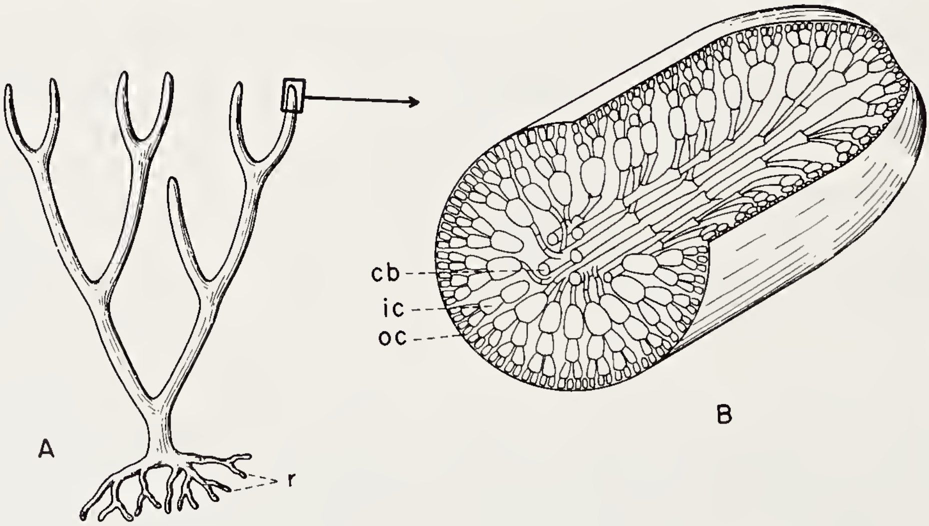

FIG. 5.13. *Furcellaria fastigiata* (Rhodophyceae). (A) General view (approx. 0.6×); (B) schematic perspective diagram of part of a thallus. cb, Central body; ic, inner cortex; oc, outer cortex; r, rhizoids.

leaf-shaped thalli of the red alga *Caloglossa leprieurii* can also on careful analysis be traced back to a branched type of thread whose branches have developed in the same plane (Fig. 5.14). The compound sporophores of the higher fungi which penetrate the soil surface and develop on top of an underground mycelium (Fig. 5.12A) consist of an irregular plexus of multiple-branched and partially cross-linked hyphae (Fig. 5.12B). This development can in many species proceed so far that sections of the sporophore look exactly like those of parenchyma tissues (pseudoparenchyma). Such pseudotissue formed by the interweaving of hyphae is generally described as a *plectenchyma.*

Tissue Thallus

The plectenchyma-type thallus leads on to the tissue thalli characteristic of many brown algae (Phaeophyceae). These differ essentially from the lichen thalli in that the segments produced by the apical cell toward the base are further subdivided by longitudinal divisions and often also by further transverse divisions. This leads to the formation of multilayered thalli, which can be round (Fig. 5.15A), bandlike (Fig. 5.16A) or of some other shape. The thallus usually develops from an apical cell, which is uniaxial in simpler forms (Figs. 5.15B, 5.16B) but

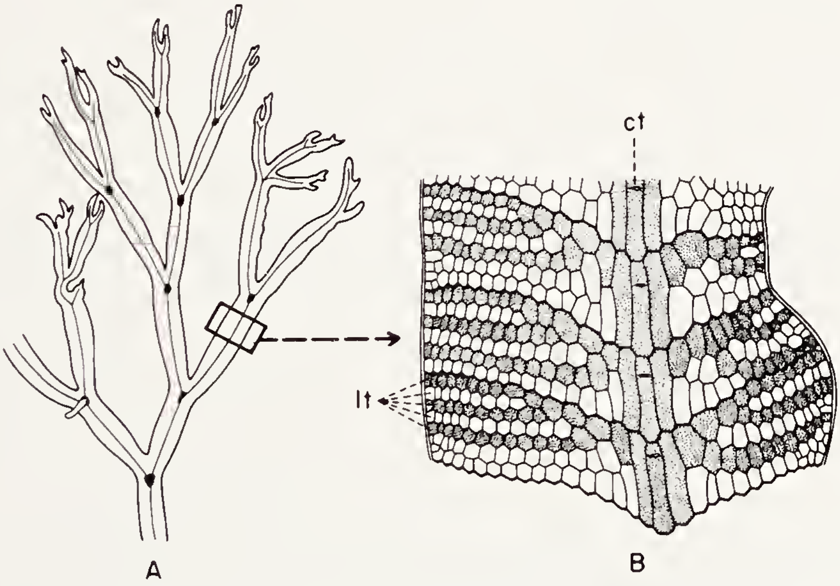

Fig. 5.14. *Caloglossa leprieurii* (Rhodophyceae). (A) General view; (B) part of the thallus (approx. 25×). lt, Lateral threads of various orders; ct, central thread. (After Cramer and Falkenberg, modified.)

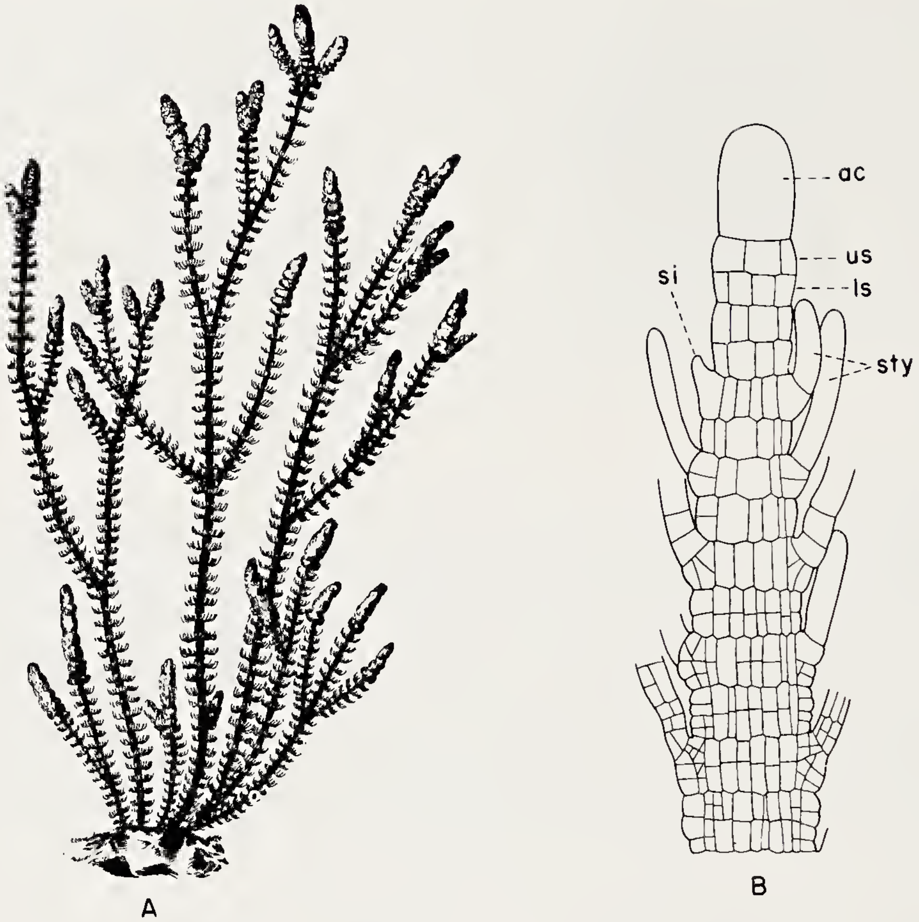

FIG. 5.15. *Cladostephus verticillatus* (Phaeophyceae). (A) General view (approx. 3×); (B) apical cell. us, Upper segment; ac, apical cell; si, initial cell of a side shoot; sty, side shoot; ls, lower segment. (After Oltmanns and Sauvageau, modified.)

can also be multiaxial in the higher ones. In certain species there are even groups of initial cells, similar to the vegetative apex of higher plants.

The branching occurs either sideways (Fig. 5.15) or dichotomously (Fig. 5.16). Dichotomy, which is the rule in *Dictyota dichotoma,* arises by a division of the apical cell parallel to the long axis of the thallus (normally the segments produced by the apical cell are watchglass-shaped), followed by growth of both as separate branches. This gives rise to the regularly branched thalli characteristic of this type.

Functionally, the cells of the tissue thalli show clear signs of differentiation. Apart from the regenerative cells produced in special organs, one can distinguish in the larger types a central pith and a peripheral cortical tissue. In *Dictyota* (Fig. 5.16E) the cells of the latter function

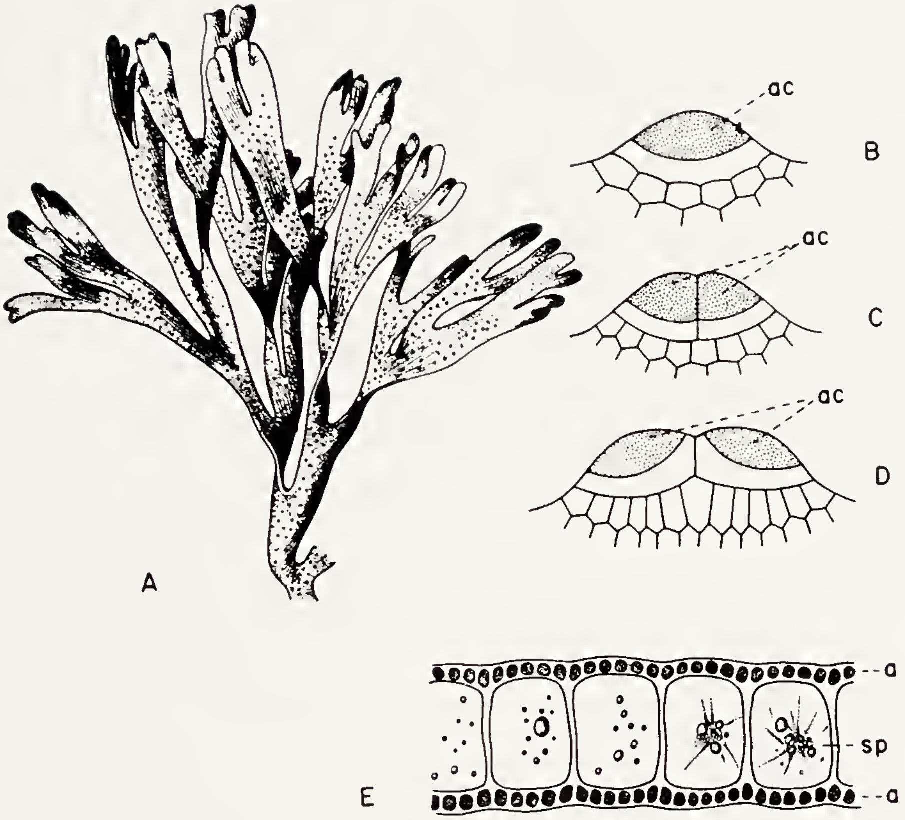

Fig. 5.16. *Dictyota dichotoma* (Phaeophyceae). (A) General view (approx. to scale); (B, C, D) apical cell in dichotomous division, schematic; (E) thallus cross section (approx. 200×). a, Assimilation cells; ac, apical cells; sp, storage cells. (After Thuret and Stocker, modified.)

as assimilation and tegumental tissues, while the inner cells function mainly as ground (fill-in) and storage tissues. In the great seaweeds, whose thalli can be up to several meters in length (in the case of the American *Macrocystis pyrifera* more than 50 meters), there is also a central vascular tissue whose elements resemble the sieve tubes of higher plants.

Bryophytes

The mosses (Bryophyta) are intermediate between the thallophytes and the Tracheophytes [Pteridophytes (ferns and fern allies) and Spermatophytes (seed plants)], which will be discussed in the next section. To some extent they still have a markedly thallous organization as shown by numerous Hepaticae and all protonemae (see p. 275). To some extent, however, they surpass them significantly, insofar as the organization of their bodies shows characteristics which lead on to the Tracheophytes; examples of this are the division into axis and leaflets. This intermediate position is related to the transition from aquatic to terrestrial life which occurs in this group. While the thallous mosses which lie flat on their substrates are restricted to very moist sites, many of the foliar Hepatieae and Musci rise into the air.

A representative of the thallous forms is the liverwort *Marchantia polymorpha* (Hepatieae), which has a bandlike flattened thallus (Fig. 5.17A). This shows a stratified structure made up of various differentiated cells (Fig. 5.17C) which serve partly as assimilation, partly as storage, and partly as tegumental tissues. They are adapted to the surrounding air by having a special aeration system built of pneumato-

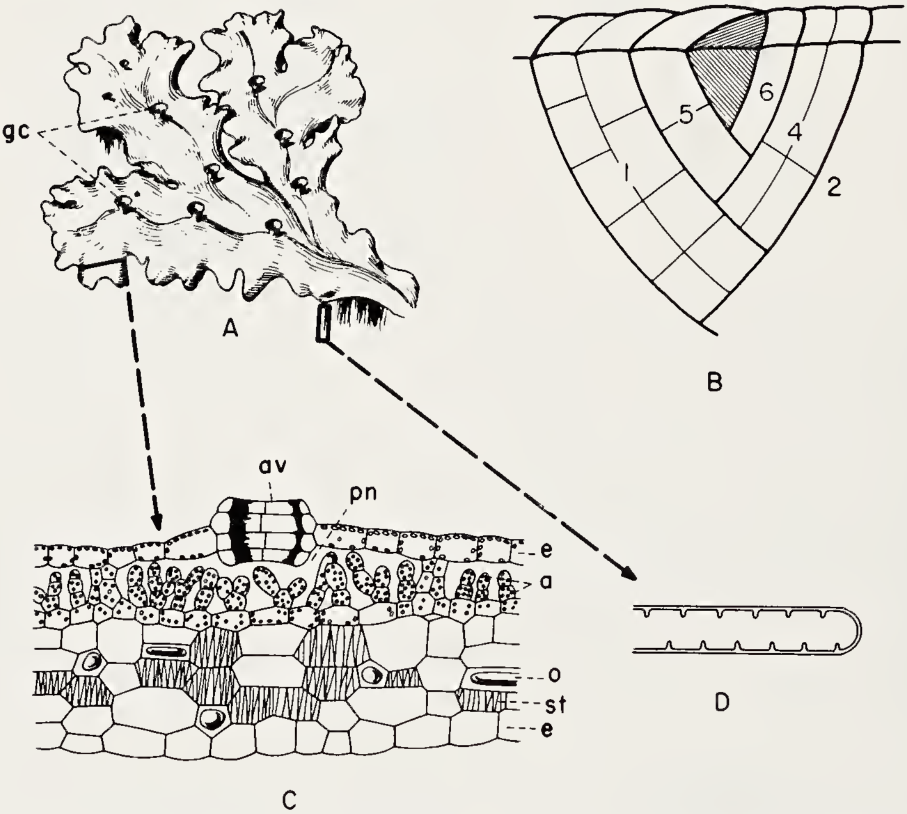

FIG. 5.17. *Marchantia polymorpha* (Hepaticae). (A) General view (approx. to scale); (B) schematic perspective drawing of an apical cell with two cutting faces, sectioned perpendicular to the surface; (C) cross section of thallus (approx. 200×); (D) conical rhizoid. a, Assimilating (cells); gc, gemma cups with brood bodies; e, epidermis; pn, pneumatophore; o, oil body; av, air vent; st, storage tissue. [(C) partly redrawn from Sacks, (D) from von Guttenberg.]

phores connected with the atmosphere through chimney-like air vents. The thalli are anchored to the ground by rhizoids (Fig. 5.17A,D), which are unicellular and should not be confused with roots. In *Marchantia* they develop conical bulges at more or less regular intervals.

The growth of such a flat thallus proceeds by way of an apical cell, with two opposite cutting faces (Fig. 5.17B). This apical cell regularly divides to cut segments off the opposite faces and the daughter cells themselves divide further to make up a stratified thallus. The branching occurs sideways by the establishment of new apical cells, and is therefore only apparently dichotomous.

The upright foliar Hepaticae and all Musci grow with a triaxial apical cell which produces segments in the direction of the base in a regular helical sequence (Fig. 5.18D,E). On further division each segment produces a leaf in addition to the ground and cortical tissues of the stem; this results in a helical phyllotaxis in which the leaflets are arranged in three vertical lines (orthostichies) (Fig. 5.18A,B). However, this arrangement is not always strictly adhered to, so that certain deviations from the basic type do occur. The leaflets are stratified, but they do not exhibit the typical structure of the foliar leaf of the higher plants (see p. 160). The small stems are anchored to the ground through multicellular rhizoids each consisting of a single row of cells (Fig. 5.18A, C). These usually have obliquely positioned transverse dividing walls. Water can be taken up over the entire surface, and the water rises in the dense carpet of moss mainly by capillary forces; there are therefore either no special tissues for water transmission at all, or they are of relatively simple structure. Truly effective transmitting tissues are found only in the most highly developed forms. In spite of their external division into shoots and leaves, the Musci therefore differ significantly from the well articulated and functionally strongly differentiated Tracheophytes.

It should be emphasized here that the lower plants (Thallophytes) that we have been discussing show variations in development of *parenchyma* cells. Truly effective supportive and conducting tissues (sclerenchyma) are only developed in higher forms, the Tracheophytes.

Tracheophytes (Pteridophytes and Spermatophytes as Opposed to Thallophytes)

The root–stem–leaf which is the organizational form of the Tracheophytes, is in its typical form suited for life on land. It is divided into

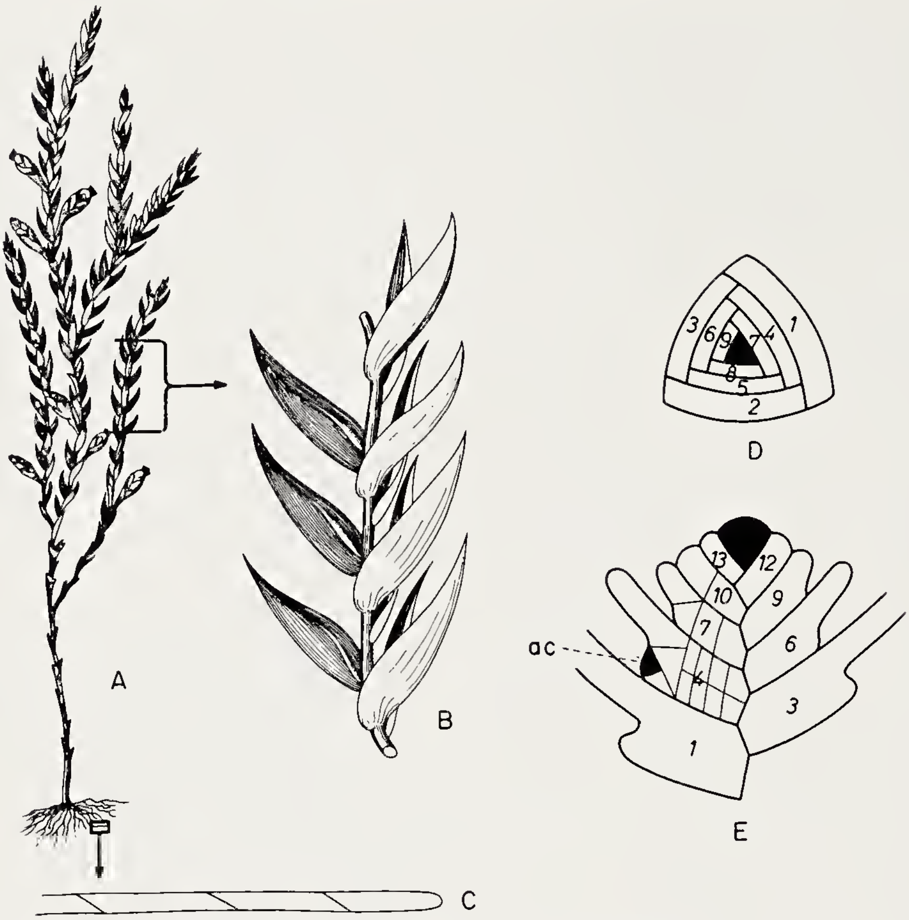

Fig. 5.18. *Fontinalis antipyretica* (Musci). (A) General view (approx. 2.5×). The small stem, normally submerged in the water, is shown in an upright position; (B) part of a shoot with leaves in three columns, schematic; (C) rhizoids with oblique transverse walls; (D) triaxial apical cell in transverse; and (E) in longitudinal section. The segments at the back are not shown. The numbering gives the sequence of the segments. ac, Apical cell layout of a sideshoot. (After Rabenhorst and Stocker, modified.)

three basic organs: true stem, leaves, and root, (Fig. 5.19A). Assimilation takes place in the leaves, whose flat shape permits optimum utilization of light. The stem bears the leaves and, owing to its upright growth and spiral leaf arrangement (phyllotaxis), there is a favorable arrangement of leaves for receiving radiation with minimum mutual shading. The stem also transports water and nutrient salts from the roots to the leaves. The uptake of water and nutrients occurs in the roots, which also serve to anchor the plant in the soil.

This division of functions is reflected not only in the external but also in the internal formation of root, stem, and leaf, e.g., in the development

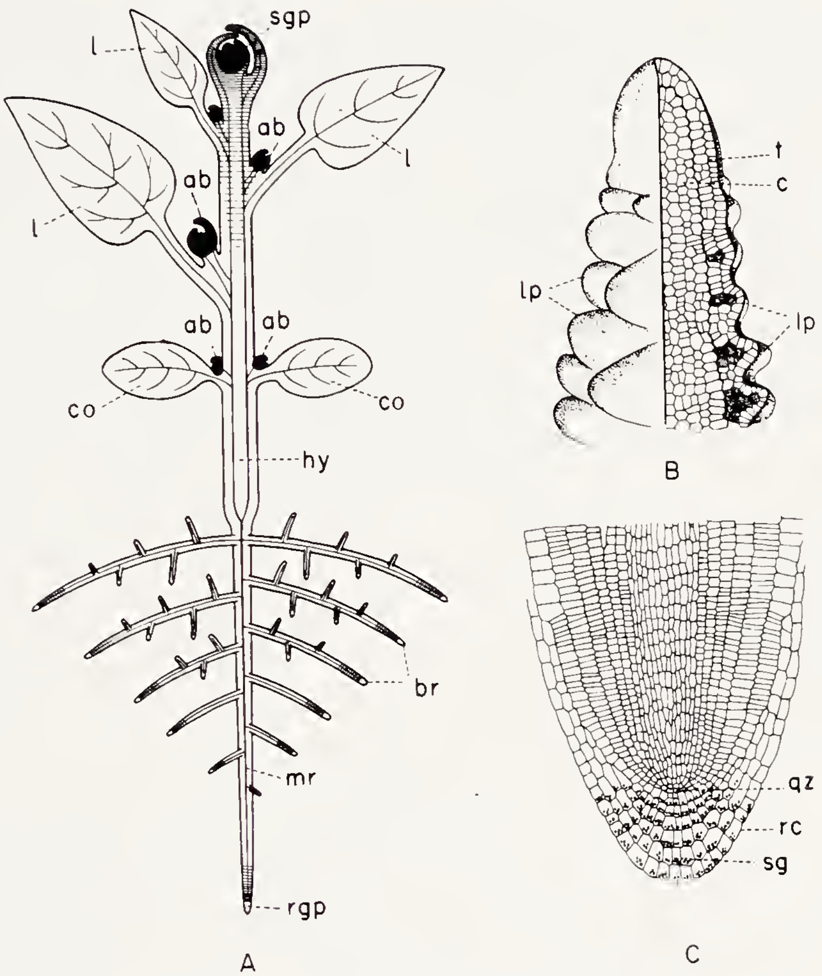

FIG. 5.19. Organization of the Tracheophytes. (A) Schematic diagram of the dicotyledon plant; (B) vegetative apex of a shoot of the water weed *Elodea canadensis;* (C) vegetative apex of a root (*Brassica rapa,* field cabbage) (approx. 70×). l, Leaf; lp, leaf primordium; c, corpus; co, cotyledon; hy, hypocotyl; ab, axial bud; sg, starch grains; br, branch roots; sgp, shoot growing point; t, tunica; mr, main root; rc, root cap; rgp, root growing point; qz, center of the quiescent zone. (After Troll, Geisenhagen, Herrig, and Kny, modified.)

of special transmission channels for water, salts, and organic compounds, in the formation of special strengthening elements allowing upright growth, etc. This distribution of functions results in the development of functionally different tissues and tissue systems whose elements have already been described (Chapter 4) and whose arrangement in the plant body will be discussed in the following chapters.

A characteristic feature of the majority of Tracheophytes is the development of special meristems on the growing points. In some pteridophytes (Equisetaceae and Polypodiaciae) there are single apical cells which are usually pyramidal (tetrahedral) with the base of the pyramid turned toward the free surface. New cells are cut in sequence off the other three faces. Some of the water ferns have three-sided apical cells with two sides from which new cells are cut off. In *Selaginella* there may be a single three- or four-sided apical cell or a group of apical cells. In all other ferns (eusporangiate) there are 2–4 apical initials. In gymnosperms a large group of apical cells divide both perpendicular (anticlinal) and parallel (periclinal) to the surface of the growing point so the cells are randomly arranged. In the angiosperm apex, apical cells are arranged with one or more outer layers overlaying a central body (corpus) of cells arranged randomly, (Figs. 6.1A, 5.19B). The cells in the outer (tunica) layers undergo only anticlinal division, while the innermost cells (corpus) divide both anticlinally and periclinally. The leaf primordia grow out and over the apex, protecting the sensitive growing point (Figs. 6.1A, 5.19A). The epidermis develops from the outermost layer of the tunica, while the remaining layers of the tunica produce the mesophyll of the leaves, the stem cortex. The corpus develops the central pith and some of the vascular tissues, and possibly some of the stele or vascular conducting tissue.

The growing point of the root (Fig. 5.19C) differs from that of the shoot in that leaf primordia are missing and that a root cap develops which protects the thin-walled meristem cells from mechanical damage by the soil. The outermost cells of the root cap die and gelatinize, and they must therefore be constantly replaced. In the pteridophytes the apical cell of the root is tetrahedral and not tri- but tetraaxial, and thus develops segments in all directions; the one at the root tip divides further and develops the root cap. In the gymnosperms the root cap is frequently not clearly distinct and it is formed from the outer initial layer by periclinal divisions. At the tip of the root-growing point of the angiosperms (Fig. 5.19C) there is a so-called quiescent center, the cells of which divide only seldom or not at all. The zone of cell division is immediately adjacent, but the regions of highest cell division activity are located at various distances from the root tip (see p. 170). The root cap is renewed by division of its inner cells. Sometimes the innermost layer of the root cap actually behaves like a meristem, and it is then known as a calyptrogen.

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Chapter 6

Internal and External Structure of the Stem

The growing points of the stem and root, which are at the opposite ends of the plant and in dicotyledons are distinctly polar, continuously contribute new cells to growth in length. These cells are produced at the two poles in opposite directions, i.e., toward each other, as a result the poles increase their separation. The differentiation that follows does not proceed at random for each cell but according to a unified plan, leading to a definite arrangement of the tissues and their cellular components. Since the stem and the root differ considerably in this respect, they will be treated separately. The stem is not built, of course, in the same manner in all plants, but the structures of the axes can be traced back to a few basic types, which will be considered in some detail.

Tissue Differentiation and Primary Structure of the Stem

The meristem at the tip of the growing point (shoot apex) retains its ability to divide from the embryonic stage of growth of the plant and it can therefore be regarded as a *promeristem.* The cells produced by it (toward the base) continue to divide further for a while, so that the upper part of the stem axis is taken up by a steadily dividing primary meristem zone; the extension of this zone in the direction of the long axis amounts only to fractions of a millimeter per day. Promeristem derivatives segregate (Fig. 6.1B) into a peripheral mantle, the *protoderm,* which differentiates into the epidermal system; the *ground meristem* differentiates into pith and/or cortex; and *procambium* (or provascular tissue) which may appear as a narrow cylinder of cells between developing pith and cortex and which retains its capacity for division perpendicular to the stem axis, later give rise to the *cambium* (see p. 137). This cylinder of procambial cells appears ring-shaped in cross section, and it is therefore known as the procambial ring with acropetal prolongations into the leaf primordia. The procambial ring may differentiate into strands called *vascular bundles* or fascicles. In gymnosperms and angiosperms the fascicles are related to leaves and are called *leaf traces.* Cells in the ring between the vascular bundles are called *primary* or *medullary rays* (Fig. 6.2).

The zone of promeristem derivatives is very short, 0.02–0.04 mm in length, and it is followed by a zone of differentiation. In this zone the ground meristem cells of the medulla or pith and cortex develop the characteristics of *parenchyma* cells, while the tegument tissue, the *epidermis,* evolves from the outermost tunica layer (Fig. 6.1A,B). The development of leaves from the second or third "layer" of cells on the flanks of the shoot apex is accompanied by the development of primary vascular tissues in the procambial cylinder. The cells in this cylinder expand longitudinally, i.e., they develop a prosenchymatous character (elongated cells with tapering ends). These cells form the so-called procambium strands, the precursors of the vascular bundles; they run parallel to the stem axis and develop branches into the leaf primordia. In the dicotyledons, vascular bundles are arranged in a ring corresponding to the shape of the meristem cylinder (Fig. 6.1A,B). In some cases, as in many herbaceous plants and creepers, the individual procambial strands are separated from each other, leading to the separation of the developing vascular bundles by bands of parenchymatous tissue, the *medullary rays* (Fig. 6.2A). In other instances they are close together, as in most woody plants (Fig. 6.2C). With increasing distance from the growing point, differentiation in the procambial strands continues. Primary xylem tissues develop on the inner side and primary phloem on the outside (Figs. 6.1A,B, 6.2A–C). The functioning of the vascular elements, the first xylem or phloem elements of the vascular tissues, is only short-lived: and the elements are

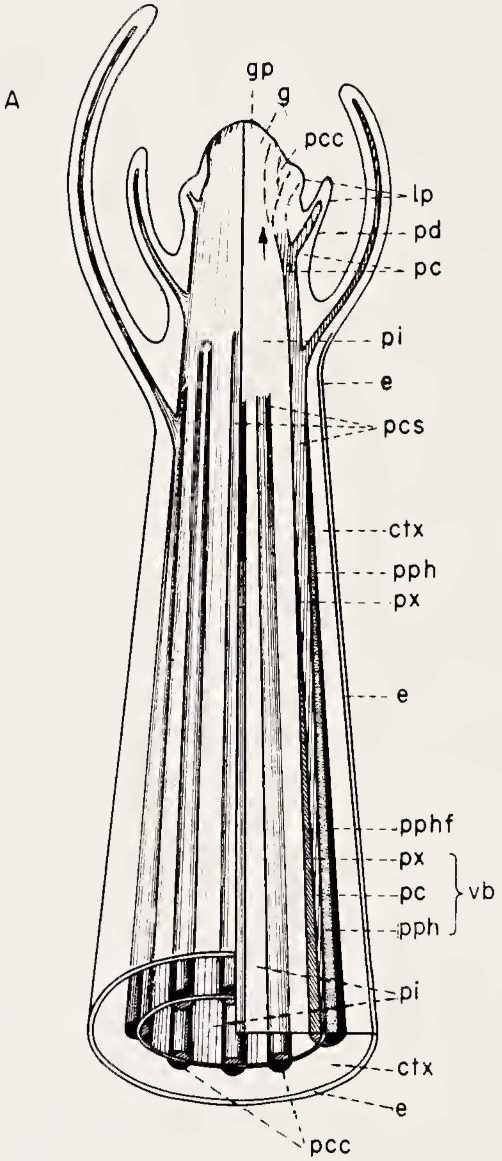
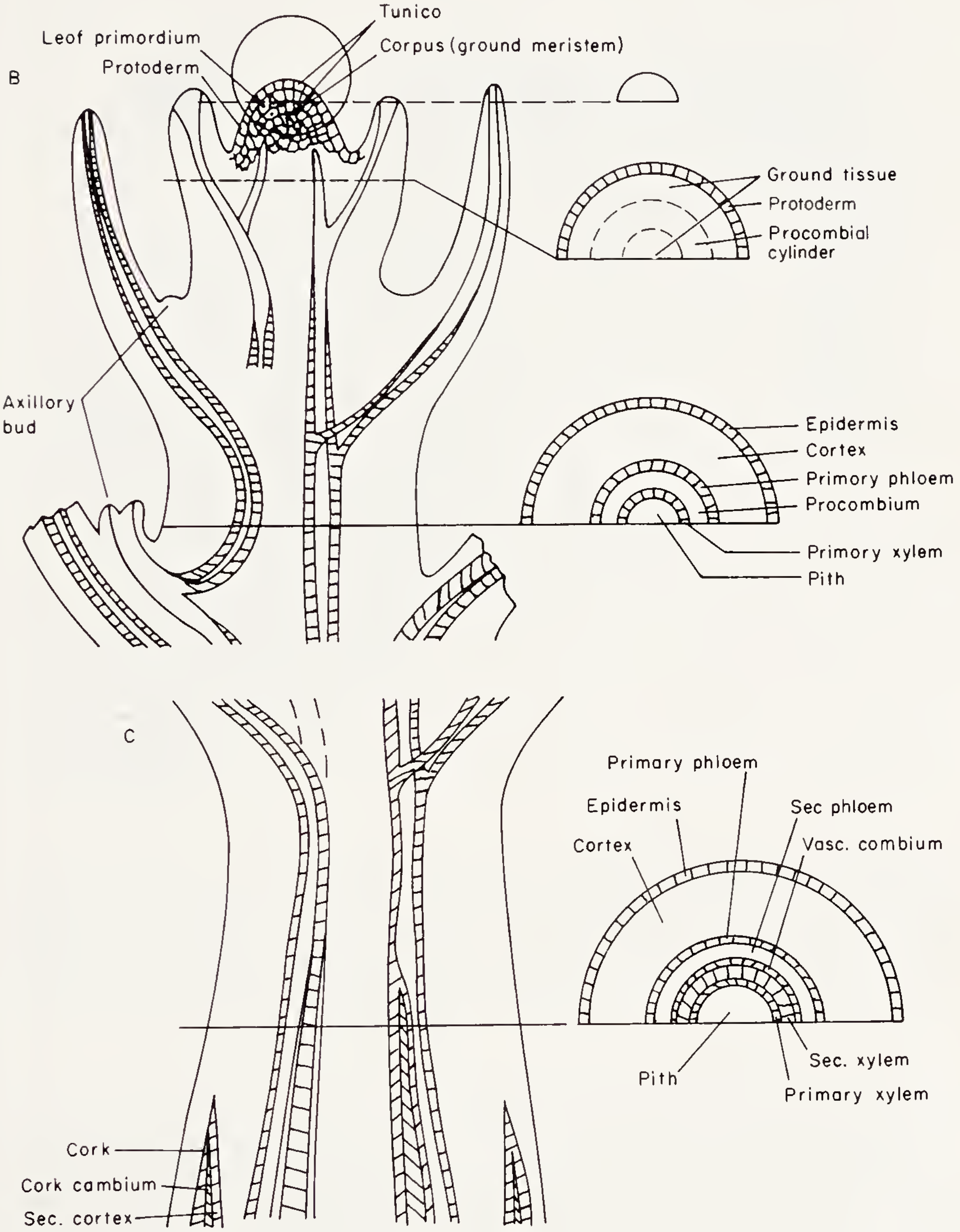


FIG. 6.1. (A) Schematic diagram of the vegetative tip of a dicotyledon. Left, in perspective; right, in longitudinal section. Only some of the vascular tissues are shown, for the sake of clarity. The sectioned vascular bundle is slightly magnified. lp, Leaf primordium; vb, (collateral) vascular bundle; e, epidermis; pcc, procambial cylinder; pphf, primary phloem fibers (if present); pc, procambium; pph, protophloem; ctx, primary cortex; pcs, procambium strand or leaf trace; gp, growing point; px, xylem (primary); pi, pith; pd, protoderm; and g, ground meristem.

(B) Diagrammatic representation of the shoot tip of a woody, dicot stem in longitudinal and transverse section. The apical meristem gives rise to the primary plant body labeled in the lower transverse section.

(C) Diagrammatic representation of the *secondary* growth in a fully differentiated older portion of a woody, dicot stem. The procambium cells change their plane of



division from transverse (growth in length by enlargement of daughter cells) to longitudinal. These cells are then called the *vascular cambium* and give rise to secondary xylem in the inside and secondary phloem to the outside of the cambium. Cells in the outer cortex may *dedifferentiate* to form a cork cambium (phellogen) which forms secondary cortex to the inside (phelloderm) and cork (phellem) to the outside. The section is a continuation of part (B).

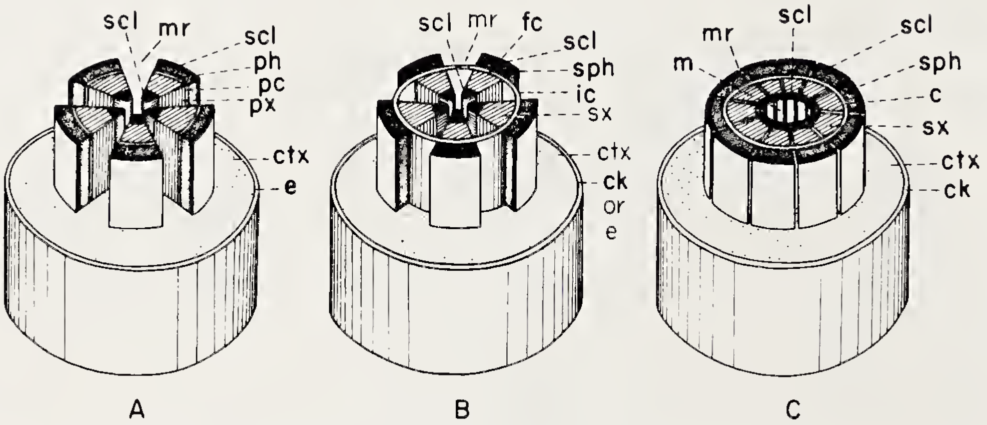


FIG. 6.2. Primary structure of the stem axis (schematic). Epidermis, cortex, medulla (pith), and medullar rays not shown in the upper parts of the diagrams. (A) Cylinder consisting of five open collateral vascular bundles separated by wide medullar rays. This pattern is characteristic of herbaceous dicotyledons. (B) As (A), but the cambium ring is closed by the establishment of an interfascicular cambium. Secondary vascular tissues are formed in the bundles from the derivatives of the fascicular cambium and secondary rays between the bundles by the activity of the interfascicular cambium. This pattern is characteristic of semiwoody dicots. (C) Closed vascular bundle cylinder. The medullar rays are narrow. This pattern is characteristic of woody stems. c, Cambium; ck, cork; e, epidermis; fc, fascicular cambium; ic, interfascicular cambium; m, medullar or pith; mr, medullar ray; pc, procambium; ph, primary phloem; ctx, primary cortex; scl, sclerenchyma elements (if present); sph, secondary phloem; px, primary xylem; and sx, secondary xylem.

torn up in the course of further elongation. The walls of primary xylem elements are usually slightly thickened, of annular, helical, or reticulate appearance (Fig. 6.3). The function of the first-formed elements is later taken over by later-formed elements of primary xylem and phloem of the vascular bundles known as metaxylem or metaphloem.

STRUCTURE OF THE VASCULAR BUNDLES

Vascular bundles are characteristic tissue systems in the Tracheophytes. They consist of two structurally different complexes: the xylem and the phloem. The xylem includes the elements of water conduction, i.e., vessels or tracheids; phloem, on the other hand, consists of sieve cells in gymnosperms and sieve tubes with companion cells in the angiosperms (Fig. 6.3). Both can be accompanied by parenchyma cells known as xylem and phloem parenchyma. The arrangement of these elements can vary considerably in the various species, so that several types of vascular bundles can be distinguished, shown schematically in Fig. 6.4.

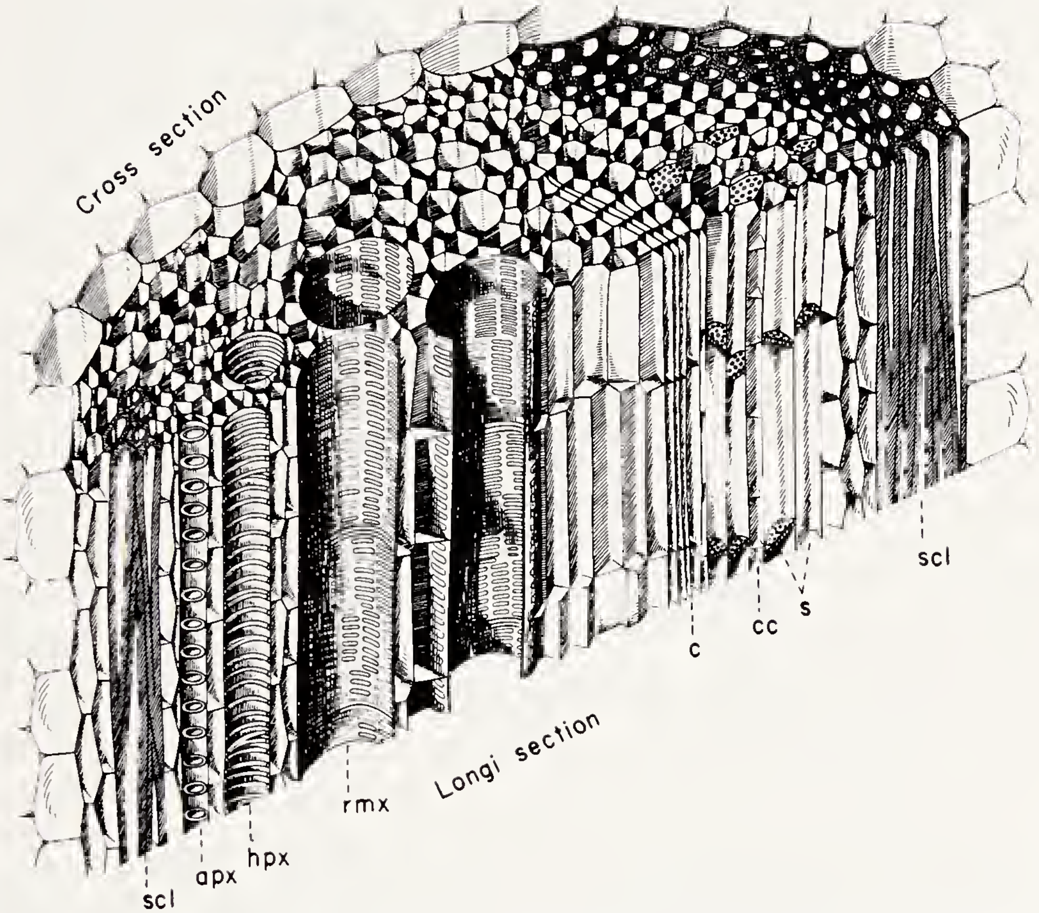


FIG. 6.3. Structure of a collateral vascular bundle in transverse and longitudinal section. cc, Companion cells; c, cambium; apx, primary xylem element with *annular* wall thickenings; s, sieve tubes, showing sieve plates on end walls; hpx, primary xylem element with *helical* or *scalariform* wall thickenings; scl, sclenchyma; rmx, metaxylem element with *reticulate* thickening. [After Mägdefrau (1951).]

In the concentric vascular bundles with external xylem (Fig. 6.4A)—characteristic of the internodes and rhizome of some monocotyledons or medullary bundles in dicots—the xylem surrounds a core of phloem cylindrically; the arrangement in the concentric vascular bundles with inner xylem (Fig. 6.4B), which occurs in most ferns, is exactly the reverse. In the collateral vascular bundles (Figs. 6.3 and 6.4C,D) which are widespread among gymnosperms as well as angiosperms, the xylem and phloem are opposite each other, with the xylem developing centrifugally from inside, and the phloem centripetally from the periphery. In the *closed* collateral vascular bundles, found in many monocotyledons, the xylem and phloem are located directly next to each other (i.e., no procambium) (Fig. 6.4C); in the open collateral bundles of gymnosperms and most

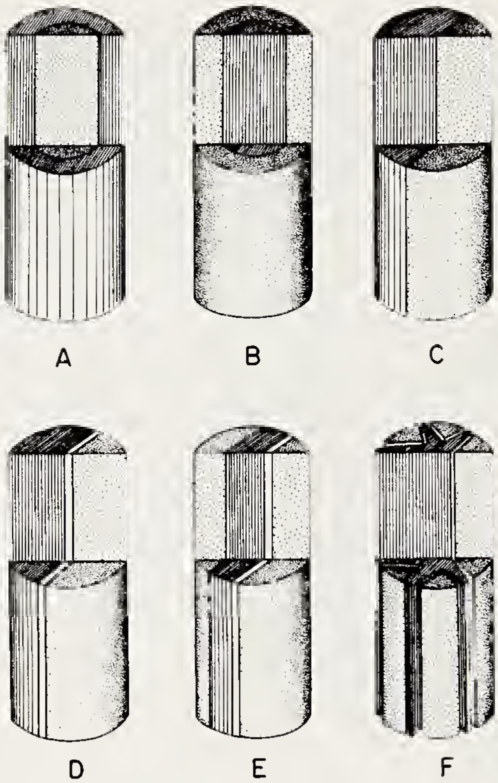


FIG. 6.4. Vascular bundle types (schematic). (A) Concentric (with xylem surrounding the phloem = amphivasal), as in monocot internodes or medullary bundles in dicots; (B) concentric (with phloem surrounding the xylem = amphicribal) as in ferns and dicot flowers; (C) collateral (a bundle having the phloem on one side of the xylem only), closed (retain no procambium after primary vascular tissues differentiate) as in lower vascular plants, the monocotyledons, and the extreme herbaceous dicots; (D) collateral, open, persistent vascular meristem (cambium) in gymnosperms and most dicots; (E) bicollateral (phloem on two sides of the xylem) as in ferns; (F) vascular *cylinder* in root where xylem and phloem strands occur on alternating radii in contrast to vascular *bundles* in the stem.

angiosperms, on the other hand, they are separated by a band of meristem tissue, the procambium (or cambium) (Fig. 6.4D). The bicollateral vascular bundles can be regarded as a special case of the collateral ones, in which the xylem is embedded between two strands of phloem (Fig. 6.4E). These are typical of some dicotyledon families (Solanaceae, Cucurbitaceae). The vascular strands in roots have a radial structure: The xylem is arranged in wedges which run radially from the center to the periphery, while a corresponding number of phloem elements are located between them (Fig. 6.4F). The number of these radii varies from case to case (in Fig. 6.4, it is five).

Normally each vascular bundle is enclosed by a sheath which consists of parenchyma cells or of strengthening elements (Fig. 6.3). The parenchyma cells are sometimes rich in starch and are then known as starch sheaths. In collateral bundles the so-called transfusion bands are found at the boundary of the xylem and the phloem; these consist of cells which have not undergone thickening, and which allow an exchange of substances with neighboring tissues.

PRIMARY STRUCTURE

The final completion of the vascular bundles and of the other tissues of the stem, which is also described as maturation, is connected with cell elongation and primary wall thickening; at the end of these processes the stem is substantially complete and fully differentiated. The vascular bundles run mainly parallel to the long axis, but they are also joined together laterally. From the place of attachment of the leaves the so-called leaf trace bundles depart from the bundles of the stem into the leaves (Fig. 6.5A); the sum total of these is known as the leaf trace. In gymnosperms and in dicotyledons the bundles are typically open and collateral, and are located on the periphery of a cylinder; they therefore appear to be arranged in a ring in cross section (Fig. 6.5A). As has

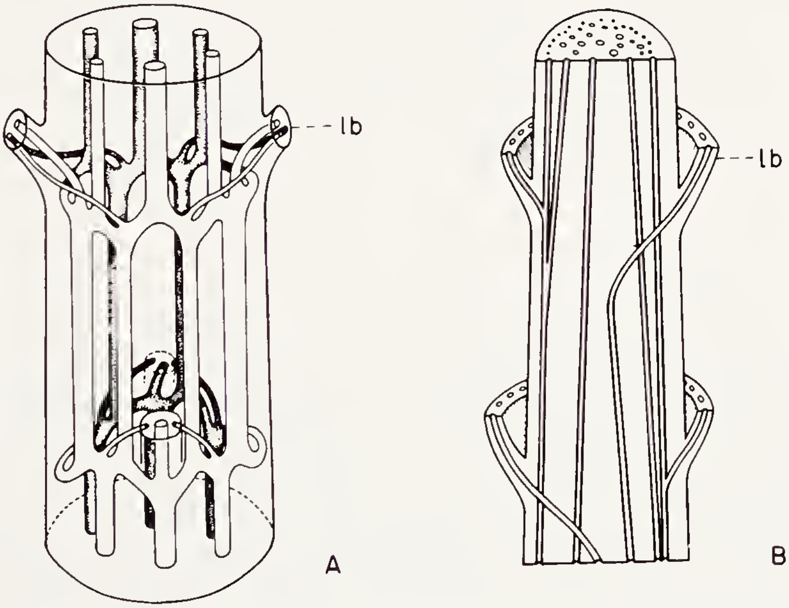


FIG. 6.5. Schematic arrangement of the vascular bundles and leaf traces in the stem: (A) in a dicotyledon with decussate phyllotaxis (*Clematis vitalba*); and (B) in a monocotyledon (palm). lb, Leaf base. (After de Bary and Rothert, modified.)

already been mentioned (p. 129), the vascular bundles can be separated by wider medullar rays or be tightly joined in a cylinder with the xylem inside and the phloem on the outside. The vascular bundles enclose the medulla or pith. The vascular cylinder is frequently surrounded by a ring of sclerenchymatous cells both inside and outside. Outside the central (vascular) cylinder (stele) is the cortical tissue; the innermost cell layer of this tissue, which adjoins the central cylinder, sometimes appears as a closed starch layer or as an endodermis. The cells of the cortical tissue contain chloroplasts in varying numbers and act both as assimilation and as storage tissues. The cortical layer is free from vascular elements except for the leaf trace bundles penetrating it. The cortical tissue is covered externally by an epidermis (or cork) which is normally free of cholorphyll. The medullary or pith cells are normally colorless, and their function is mainly that of storing reserve materials. Frequently they are later torn up or grow apart, which leads to the formation, lysigenously (origin by cell dissolution) or schizogenously (origin by separation of cell walls), of a medullary or pith cavity.

Apart from the vascular bundles, the primary strengthening elements are also completed in the course of differentiation and ripening. These strengthening elements can be sclerenchymatous or collenchymatous in character. The occurrence of sclerenchymatous fibers in the sheaths of the vascular bundles (Figs. 6.2C and 6.3) has already been mentioned. Moreover, strengthening elements can also be found outside the central cylinder, either forming a closed cylinder or as individual wedges. These can be either collenchymatous or sclerenchymatous. The principally peripheral arrangement of the strengthening elements in young shoots is essential for bending strength.

Secondary Thickening

The primary tissues produced in the course of differentiation, maturation, and growth in thickness are often so constructed that they are able to provide the leaves formed in one growing season with water and mineral salts, and also impart the required stiffening to the stem. Sometimes, however, the body of the plant expands considerably in one or several growing seasons, as is the case with trees, shrubs, and many semiherbaceous plants. The primary vascular elements can then no longer provide sufficient water supply, and the strengthening elements are inadequate to support the branch structure which in trees often projects far out from the trunk. The development of secondary conducting and strengthening

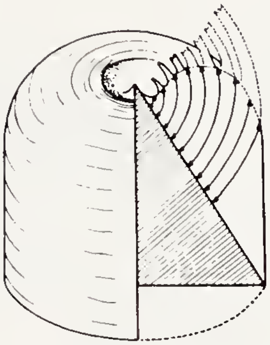


FIG. 6.6. The vegetative apex in a palm at the base of an apical cavity (schematic). Left, in perspective; right, in cross section. The leaf shoulders are shown only in cross section. The shaded cone in the section shows the initial condition, while the double arrows show the main direction of growth of the meristem mantle.

tissues is then necessary, and this occurs in the course of the secondary (cambial) thickening.

The only exceptions to this rule are the tree ferns, cycads, and certain treelike monocotyledons. In these, the vegetative apex undergoes a marked expansion due to the formation of an apex mantle of periclinally dividing meristem cells. This produces a crater-shaped hollow, the vegetative apex being located at the bottom of this hollow (Fig. 6.6) and predetermines the final stem thickness; in subsequent elongation the stem rises as a column of sclerified leaf bases of approximately uniform thickness and lifts the tuftlike leaf rosette. Sufficient conducting and strengthening elements are here available from the outset, and no secondary thickening is therefore necessary.

The secondary thickening of the gymnosperms and of the dicotyledonous angiosperms occurs by means of a meristem, the vascular *cambium.* This is either derived from a primary meristem, the procambium, (Fig. 6.1C), or it may happen that only the so-called fascicular cambium, located in the open collateral vascular bundles, is of primary origin and forms secondary xylem and phloem cells. The remaining cells in the stem cross section, which are medullar ray tissue between the vascular bundles may regain their ability to divide and therefore constitute a secondary meristem (interfascicular cambium) which produces secondary ray cells (Fig. 6.2B). This pattern is characteristic of semiherbaceous dicots. In woody plants a closed cylinder of cambium initials and their derivatives originate from the procambial ring (Fig. 6.2C), these cells being approximately prismatic, mostly pointed at the ends (Fig. 6.7), and divided by tangentially arranged walls. The freshly formed cells are cut off either to the inside or outside during this process to form pre-

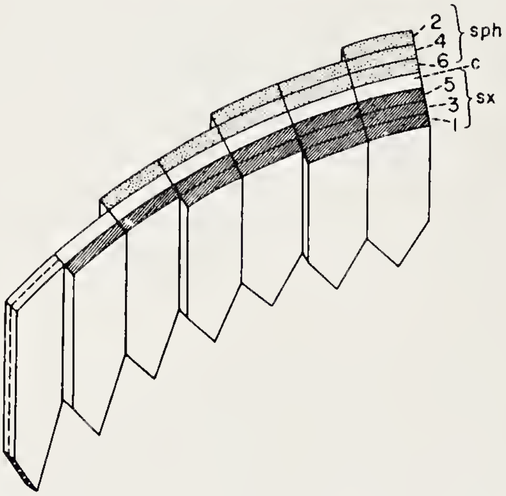


FIG. 6.7. Schematic representation of the division process of the cambium. The prismatie cells, pointed at the ends, are cut transversely at the top. c, Cambial zone; sph, secondary phloem (dotted); sx, secondary xylem (shaded). The numbers show the sequence of cell development.

sumptive elements of the xylem or phloem. Actually the cambium produces three cells or more on the xylem side to one on the phloem side. A continuous zone of initial cells is, however, preserved in the process, but not as a single layer of cells as represented schematically. Continued production of new cells toward the inside results in a steady increase in the girth of the shoot axis.

By definition, all tissues developed on the inside of the cambium are described as wood (secondary xylem) irrespective of the degree of lignification; while those on the outside are known as secondary phloem. In the region of the vascular bundles secondary xylem or phloem elements are produced, while parenchymatous elements are formed in the region of the medullary rays. The primary medullary rays are steadily lengthened in this way and extend from the medulla to the cortex. In addition, further so-called secondary rays are produced during the continued growth of the stem in girth; these originate in the secondary xylem and phloem, respectively (not extending from pith to cortex) and serve as "fill-in tissue" between files of xylem and phloem elements during radial expansion (Fig. 6.8).

WOOD

Wood is secondary xylem. The elements of wood include the vessel members, tracheids, wood fibers, and also xylem and medullary ray parenchyma. The cells produced from the cambium must undergo

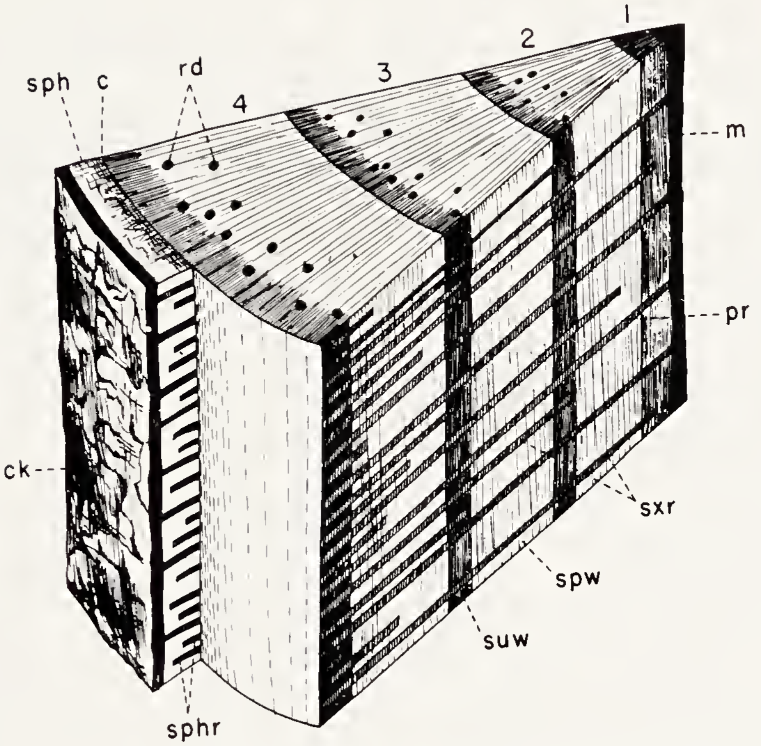


FIG. 6.8. Part of a four-year-old *Pinus* stem, section cut in winter. Bark: sph, secondary phloem; ck, cork. c, Cambium; spw, spring wood; rd, resin duct; m, medulla or pith; sphr, secondary phloem ray; suw, summer wood; sxr, secondary xylem ray; pr, primary ray; 1,2,3,4: successive annual rings. (After Schenk.)

thorough transformation, corresponding to the element that they are building; as shown in Fig. 6.9, the types of growth involved can vary considerably—cell division, cell elongation, modification of cell wall, loss of protoplast. Differential growth in spring and summer results in annual rings (Figs. 6.8 and 6.10).

The vessel members have perforated end walls and simple or bordered pits on the side walls (Fig. 6.9). Pits connecting two tracheids are bordered from both sides (Figs. 3.17 and 6.10); pits connecting vessels with parenchyma cells are bordered only from one side. While the wide vessels (Fig. 6.9) serve only for the conduction of water, the tracheids have both conductive and strengthening functions. The walls of the latter type are strongly thickened and their lumens are narrow. Wood fibers are typical sclerenchymatous fibers as shown by their uniformly thickened walls with simple or obliquely positioned pits and extreme length. Finally, the wood and medullar ray parenchymatous cells are rectangular and slightly elongated radially (Fig. 6.9). They retain their living contents and serve partly for storage of the reserve materials and partly for transverse conduction. Their walls are generally only slightly thickened.

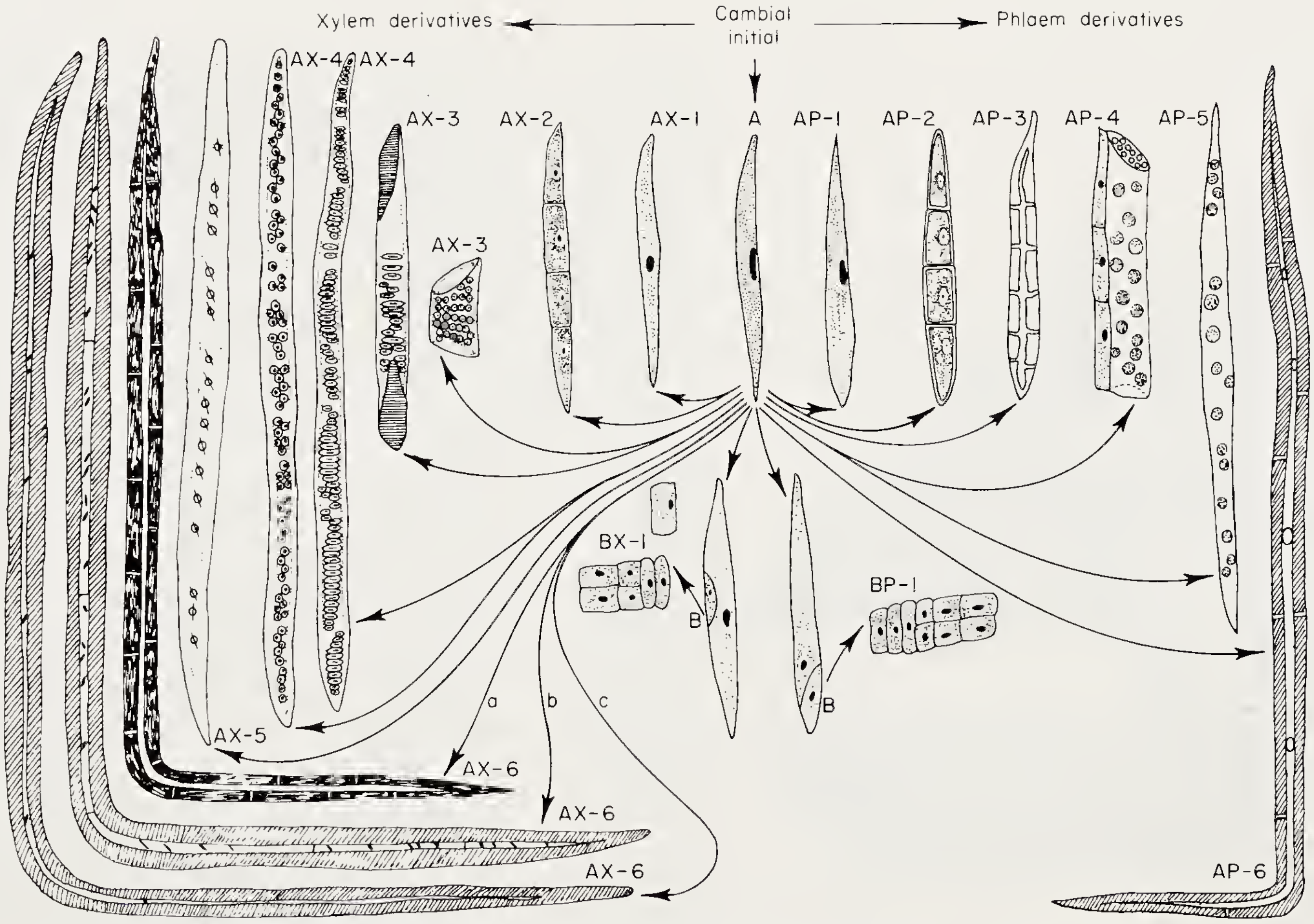


Fig. 6.9. Diagrammatic representation of xylem and phloem cell derivatives from ray and cambium initials. Gymnosperms have more different specialized cell types than do angiosperms. Many cell types, such as periderm, laticifers, and idioblasts, have not been included here. Cells may retain their protoplasts at maturity or not. [Modified from Esau (1953, 1960).] See p. 141 for further detail.

There are significant differences between plant species in regard to the role of the basic elements in the wood structure and their arrangement. These differences are especially obvious between gymnosperms and angiosperms so one representative from each of these two groups will therefore be described.

The Scots pine (*Pinus sylvestris*) will serve as the typical gymnosperm; the wood of these plants has a simpler structure than that of deciduous trees. In the gymnosperms the tracheids act both as reinforcing and as conduction elements. Both wood fibers and vessel members are therefore absent. Even the wood parenchyma is usually little developed in Pinaceae, Taxaceae, and Araucariaceae (Esau, 1960). In *Pinus* it consists only of the gland epithelium which lines the resin ducts. The branched network of resin ducts penetrates throughout the trunk. In the yew (*Taxus baccata*) the wood parenchyma is missing altogether. Following the course of the rays (Fig. 6.8), the cells of the ray parenchyma are radially extended (Fig. 6.10 tangential section) and are so arranged vertically that the rays have the width of only one cell (Fig. 6.10, tangential section). In *Pinus* the upper and lower rows of ray cells may contain transverse ray tracheids. They facilitate the transport of water in radial directions. In contrast to the simple pits of the other ray cells, the pits of the transverse tracheids are half-bordered with the border on the side of the tracheid. While there are no intercellular spaces between the tracheids, the ray cells are

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FIG. 6.9. *(Continued)*

The vascular cambium contains two types of cells: (A) fusiform initials, elongated cells with tapering ends which give rise to the longitudinal (long axis) systems of xylem and phloem; (B) ray initials, small, nearly isodiametric cells elongating radially and giving rise to the ray cells of xylem and phloem. New ray initials originate from fusiform initials by either subdivision of a fusiform initial, by cutting off the tip of a fusiform initial, or by the phragmoplast intersecting the same wall to cut out a small lens-shaped piece of the fusiform initial. The phloem rays (BP-1) are continuous with the xylem rays (BX-1) since both originate from a common group of ray initials in the cambial region.

On the xylem side of the vascular cambium, derivatives of the fusiform initials form, for example, xylem parenchyma cells (AX-1) and xylem parenchyma strands (AX-2), vessel members (AX-3), and/or tracheids (AX-4), fiber tracheids (AX-5), and fibers (AX-6) [(a) mucilaginous, (b) septate, (c) libriform].

On the phloem side of the vascular cambium, derivatives of the fusiform initials may form, for example, phloem parenchyma cells (AP-1) or phloem parenchyma strands (AP-2), sieve tube members with companion cells (AP-4), or sieve cells (AP-5), sclereids (AP-3) and extraxylary fibers—variously called phloem, cortical, pericycle, or bast fibers (AP-6). Crystal formation may occur rather commonly in phloem parenchyma cells or strands. Sclereids are represented by several categories of thick-walled cells with transitions between categories and polymorphism within categories.

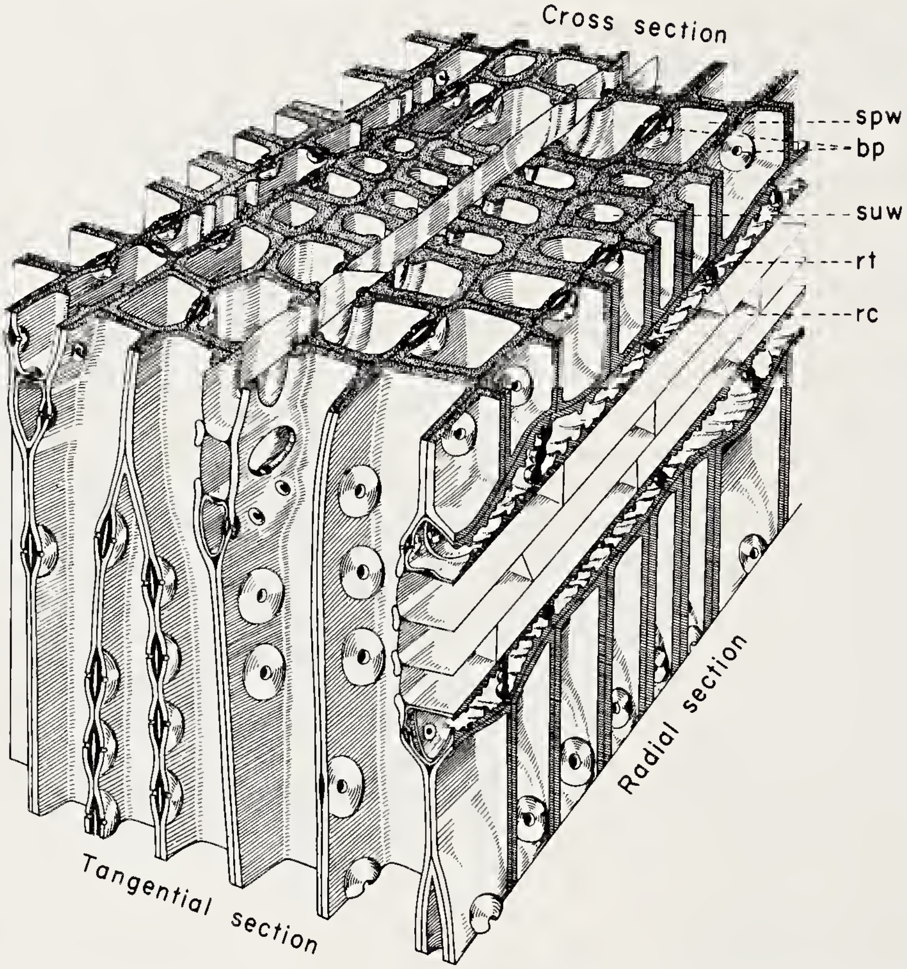

FIG. 6.10. Wood of the Scots pine (*Pinus sylvestris*). spw, Springwood; bp, circular bordered pit on tracheid; rc, ray cells; rt, ray tracheids; suw, summerwood. [After Mägdefrau (1951), modified.]

separated by an intercellular system connected with the phloem and the cortex.

A cursory examination of the cross section through pine wood (Figs. 6.8 and 6.10) reveals that the tracheids with wide and narrow lumens alternate in regular manner. These annual rings, visible to the naked eye, are a result of the annual periodicity in the activity of the cambium (see p. 358). The cambium starts its activity in spring by producing tracheids with wide lumens (spring wood), while the lumens of tracheids formed later in the growing season become progressively narrower (summer wood). Finally the cambium stops functioning altogether, and starts up again the next spring with the production of cells with wide lumen. This gives rise to a well-defined annual boundary. The tissues located between two such boundaries correspond therefore to one year's growth, so that the age of a tree can be estimated with some accuracy from the number of annual rings. In tropical woods, growth is not subject to strong annual fluctuations, several rings, only weakly developed, may be formed annually or be completely absent, since periodicity of wood formation is related to wet and dry periods in the tropics.

A corresponding annual cyclic arrangement of the tissues can also be found in the deciduous trees in the middle latitudes. The silver birch (*Betula alba*) may serve as an example (Fig. 6.11). However, the regular arrangement of the individual elements is here disturbed by vessel members with wide lumens. These are large vessel members, with perforated transverse end walls and pitted (simple or bordered) side walls. Vessels with wide lumens may be formed preferentially in spring, in which case they are arranged in rings on a cross section. These are known as ring porous woods, e.g., the oak (*Quercus*), ash (*Fraxinus*), and elm (*Ulmus*). In diffuse-porous woods, such as the birch (*Betula*), beech (*Fagus*), poplar (*Populus*), or basswood (*Tilia*), vessels with wide lumens are formed

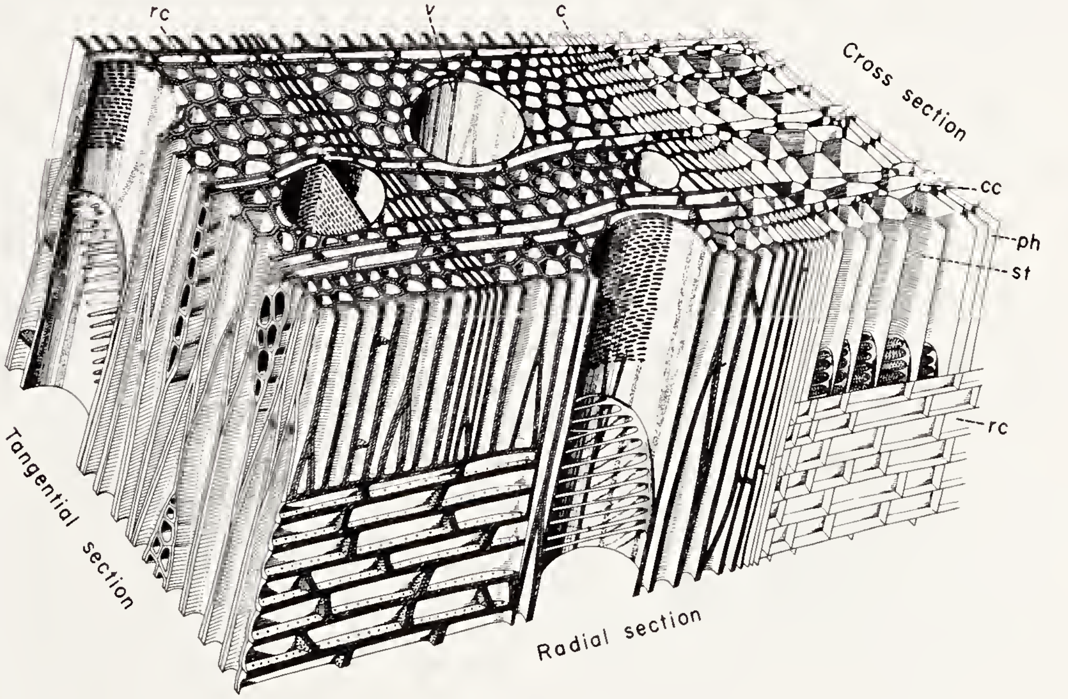

Fig. 6.11. The xylem and phloem of the birch (*Betula alba*). cc, Companion cells; v, vessels; c, cambium; ph, collapsed sieve tubes; rc, ray cells; st, sieve tube. [After Mägdefrau (1951), modified.]

throughout the growing season and are more or less evenly distributed over the whole cross section. The other elements of wood occurring in addition to the vessels include wood fibers, wood and ray parenchyma, and often tracheids as well (Fig. 6.11). The wood parenchyma occurs in strands arranged lengthwise or tangentially and in the latter case interconnects the rays.

The vessels and tracheids are active over only a few growing seasons. Transmission of water then proceeds only through the outer annual rings, the so-called sapwood, while the oldest (innermost) annual rings (heartwood) are put out of action. Their only remaining functions are to strengthen the trunk and serve as reservoir for waste products. The vessel lumen often becomes blocked by tyloses, wood parenchyma cells which penetrate the vessels through the pit areas. The cell walls can be protected from microbial attack by the deposition of tannins and other compounds. This is frequently accompanied by a dark coloration by which the so-called heartwood is easily distinguished from the sapwood. Such deposition improves both the mechanical properties and durability of the wood and thereby its value (teak, ebony). In some trees, e.g., in basswood, poplar, and willow (*Salix*), there is no corresponding change from sapwood to heartwood, and these trees therefore are more susceptible to rotting.

PHLOEM

In accordance with its function, the conduction of organic substances (e.g., sugar), the phloem contains first of all the sieve cells (gymnosperms) of sieve tubes (angiosperms) which in the dicotyledons[1] are accompanied by companion cells. Sclerenchymatous elements (the phloem or bast fibers) are also present as is phloem and ray parenchyma (Fig. 6.11). Due to the annual periodicity in functioning of the cambium, annual rings can in a few cases (larch) develop in the phloem fibers, too. Normally, however, no annual rings can be observed; instead, the cambium produces alternately hard bast (phloem fibers) and soft bast (sieve tubes, companion cells, parenchyma). The sieve tubes are active typically over only one growing season, seldom over a few. The secondary rays produce the continuation of the wood medullary rays, as has already been mentioned.

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[1] As has already been mentioned (see p. 87), companion cells also occur in monocotyledons. Monocots do not undergo a secondary growth of thickness in the true sense of the word (see p. 146); they also have no stem phloem fibers but bast fibers in leaves.

Finally, resin ducts (e.g., in conifers) or other glands can also occur in the phloem.

The originally regular radial arrangement of the phloem elements is thoroughly disturbed during the secondary growth in thickness, and the cortical tissue expands tangentially to the shoot axis with increasing girth of the stem. This leads to destruction of the cortical and phloem tissue since the phloem elements do not follow the increase in girth with an expansion of their own, being divided only from time to time by radial walls. Such expansion growth can be observed especially in the medullary rays of many woods, which can expand outward like wedges (lime).

PERIDERM

The stem epidermis is suited to rapid radial expansion only in certain cases, e.g., in the rose and the maple. Most frequently it cannot keep up with the increase in girth and is broken up. It must then be replaced by secondary tegumental tissue. This is produced by a special meristem layer, the *cork cambium* or *phellogen,* which is produced either by the epidermis itself (Fig. 6.12A) or, more frequently, from cortical cells situated below the epidermis or even further inside (Figs. 6.1 and 6.12B). The formation of phellogen occurs with the onset of the secondary growth in thickness, but sometimes even earlier. The cells of the phellogen divide tangentially, and produce regular rows of cells to the outside which are known as *cork* (phellem) (Figs. 6.1C and 6.12) whether or not they have suberin deposited in them. Cells without suberin are produced to the

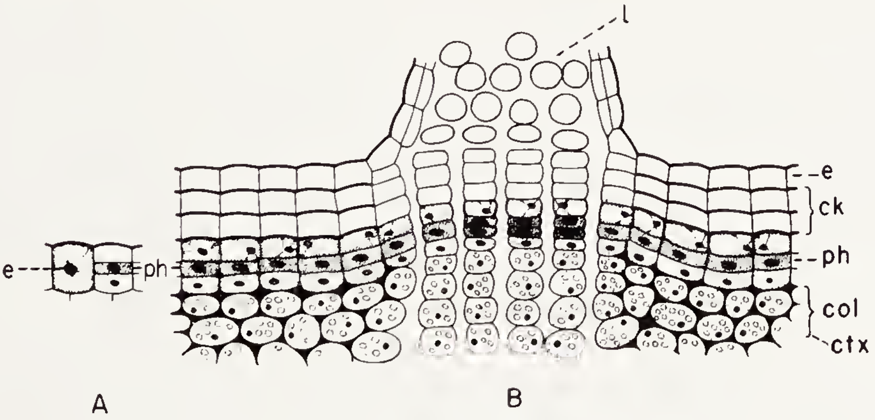

Fig. 6.12. The periderm of an apple tree: (A) establishment of the phellogen in the epidermis; (B) section through the periderm with lenticel. e, Epidermis; ck, cork; col, collenchyma cells; l, lenticel; ph, phellogen; ctx, secondary cortex. [After Mägdefrau, from Stocker (1952, p. 77).]

inside of the phellogen in smaller numbers, these make up the phelloderm or secondary cortex. Cork, phellogen, and phelloderm are known collectively as the *periderm.*

As has already been said (see pp. 83, 85), the cork cells are lined with suberin lamellae. This leads to a cutoff of the supply of water and nutrients, so that both the cork cells themselves and most tissues outside the phellogen die off. The cork tissue is also largely impermeable to air, and therefore in the absence of special ventilation pores all exchange of gases between the stem tissue and the environment would come to an end. However, ventilation pores are presently known as *lenticels* which are produced above the medullary rays more or less simultaneously with the beginning formation of the periderm to replace the former stomata. The phellogen increases its reproductive activity locally and produces many loosely packed cells in contrast to cork, which lift up the tissues above them and finally break through (Fig. 6.12B). The lenticels are rich in intercellular spaces, enabling easy exchange of gases.

BARK

With the exception of a few cases in which the first cambium layer remains permanently active (cork oak, beech), the bark soon stops dividing and is cut off by a second one produced in a deeper cortical layer. This too is active only for a limited time being replaced by a third, deeper one, and so on. The cork cambia are therefore deposited quite soon not in the primary cortex but in the phloem. The outer tissues of the cortex and of the phloem, known collectively as *bark*, are separated in this manner by the periderm layers. Tissues of cork cambia, which run approximately parallel to the trunk perimeter, forming enclosed cylinders, are known as *ring bark* (Fig. 6.13A), which occurs, for example, in vines. Tissues in which the cork cambia surround separate regions and terminate in older periderm layers are known as the *rhytidome* (Fig. 6.13B), which occurs, for example, in pines or oak. The outermost, i.e., oldest parts, of the bark become mostly fissured and can peel off. Regular separating layers develop in many trees (planes, pines), along which the bark is cast off.

The Growth in Thickness in Monocotyledons

In some monocotyledons with trunks, e.g., in *Dracaena* (dragon tree), there is a type of secondary growth in thickness quite different from the one described above. A cylinder of meristem cells is formed in the inner cortical layers, which produces complete vascular bundles and lignifying

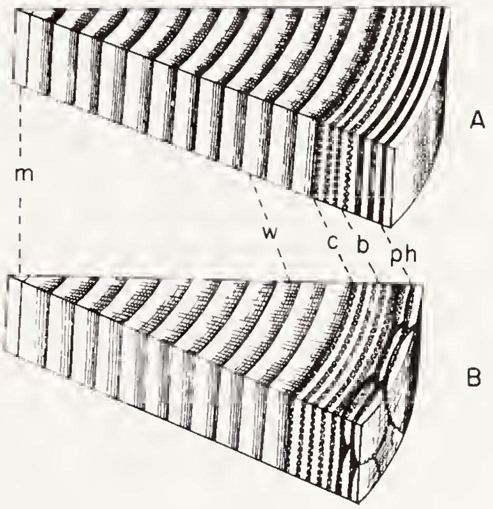

FIG. 6.13. Schematic formation of the bark. (A) Ring bark (rhytidome from successive cambia uniform about the stem); (B) rhytidome (outer bark, mostly periderm and derivatives). b, Secondary phloem (inner bark); c, cambium; w, wood (secondary xylem); m, medulla (pith); ph, phellogen. [Partly after Mägdefrau (1951.)]

parenchyma inward, and parenchymatous cortical tissue outward. The vascular bundles are therefore in this case distributed over the whole cross section of the central cylinder.

Morphology of the Stem

In the simplest case the stem consists of an upright column bearing leaves having a terminal vegetative growing point. The places of attachment of the leaves are the nodes, and the intervening stem sections are called internodes. The section below the first leaves (cotyledons) is known as hypocotyl (Fig. 5.19A); the cotyledons mostly die off later (see p. 159). The internodes can elongate, even after completion of leaf differentiation by intercalary growth, which is persistent meristematic activity at the base of the internode. In any case, the activity of these intercalary growing zones is mostly of limited duration. Intercalary growth is, however, very marked in grasses, e.g., in cereals, in which the intercalary growing zones are found at the lower ends of the internodes (Fig. 6.14). Their cells are thin walled, and so the stem is protected over the lower parts of the internodes by a tubelike sheath which develops out of the lower part of the primordium of the corresponding foliage leaf. In addition, the base of the lower part of the leaf primordium thickens into a solid node. In the

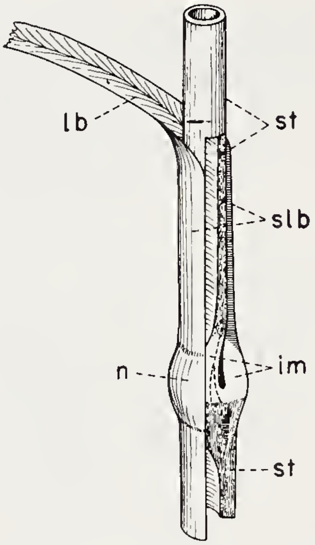

FIG. 6.14. Part of a cereal stem, partly in perspective and partly in cross section. im, Intercalary meristem; n, nodes; lb, upper leaf blade; st, stem; slb, sheathlike leaf base. (After Rauh, modified.)

absence of internodal growth a leaf rosette develops, such as that of the plantain (Fig. 7.3).

A series of plants exhibit such monoaxial growth, but in the majority of cases the pattern on which the plant body is constructed is much more complicated.

BRANCHING

In the Tracheophytes, just as in the lower plants, branching can occur both dichotomously and sideways. However, dichotomy is restricted to the club mosses (Lycopodiaceae) and related plants (Pteridophyta), while all living Tracheophytes branch exclusively sideways. In the typical case the side shoots develop from the external tissues of the stem, i.e., exogenously, in the leaf axils from bud primordia (Fig. 6.1A). They are therefore described as axillary shoots, and the corresponding leaves as bracts or subtending leaves. They are found first as quiescent growing points (axillary buds) in the leaf axils, and either start to grow soon or remain quiescent (dormant) for a long time depending upon their position on the stem. In the angiosperms each foliar leaf carries an axillary bud, while in the gymnosperms only some of the leaf axils form axillary buds. Apart from these "normal" sideshoots, so-called adventitious shoots also occur. These are formed on the stem, leaves, and roots: Parts of differentiated tissues regain their ability to divide and produce new growing points, as is known to happen in cuttings. In many cases accessory buds occur along with the main axillary ones, which are located either above (serial accessory buds) or next to each other (collateral accessory buds).

If the side branches grow slower than the main axis, the growth is said to be *monopodial* (Fig. 6.15A). Typical examples among the trees are spruce (*Picea*) and fir (*Abies*). The ash (*Fraxinus*) and the oak (*Quercus*) also divide monopodially, but the main axis stops growing at a later stage of its development. The sideshoots may branch further, and they can then be assigned of 1, 2, 3, etc. Even here, however, the side branch of a higher order is less developed than the one whose axillary shoot it represents. Often, however, the reverse happens: The main axis is left behind in growth by the development of the side branches, or stops growing altogether. This type of branch system is known as a *sympodium*. The growth may then be restricted to only one of the two side branches, giving rise to a monochasium (Fig. 6.15B), which often produces an apparently monopodial axis. Alternatively, more than one side branch may continue to develop giving rise to a dichasium (Fig. 6.15C) if two branches develop, or to a pleiochasium if more than two branches develop. Characteristic examples of monochasia are the shoots of the grapevine (*Vitis vinifera*) and the rhizoms of Solomon's seal (*Polygonatum multiflorum*, Fig. 6.17F); examples of dichasia are the shoot axes if lilac (*Syringa vulgaris*) and the mistletoe (*Viscum album*, Fig. 13.1).

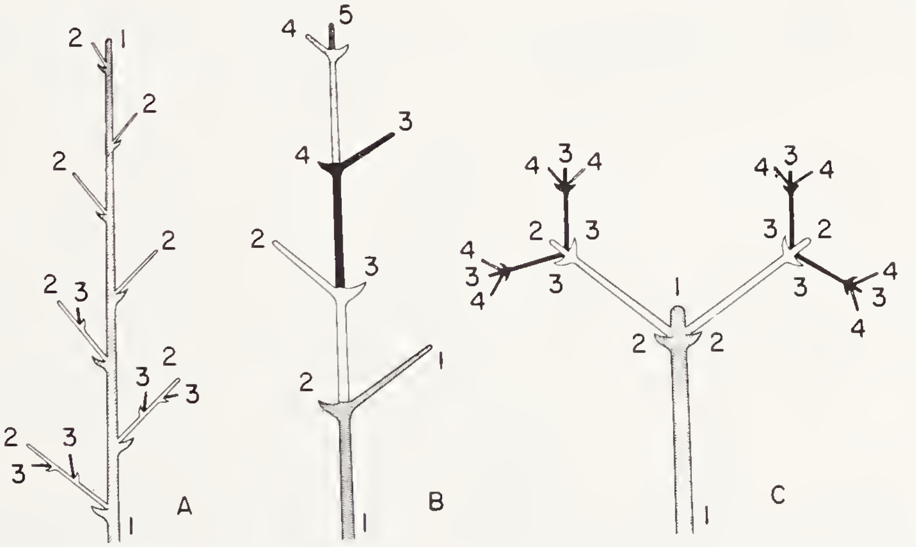

FIG. 6.15. Schematic branching types. (A) Monopodium; (B) and (C) sympodium: (B) monochasium; (C) dichasium. The numbers refer to the sequence of axes.

In any case not all side shoots are equally involved in the formation of the branch crown (only some of them grow to become long shoots), while the majority remain short and do not branch further. They mostly serve as carriers of foliage, as shown by the example of the pine (Fig. 6.16).

There are also some differences between the symmetries of the shoot axes. Upright (orthotropic) shoots normally have radial symmetry, while the more or less horizontal (plagiotropic) ones are usually dorsiventral.

In regard to the shape and the structure of the stem, and also its life-span, we can distinguish: (1) annual herbs, which are usually not lignified and die off at the end of one season; (2) biennial herbs which produce a vegetative stem one season which dies back and then produces a flowering stalk from the root the second season; (3) perennial herbs, whose epigeous parts are not lignified and die off at the end of the growing season. They survive winter either with the aid of hypogeous organs (geophytes, see p. 167) or with shoots lying close to the ground, covered with snow in winter, with epigeous dormant buds (hemicryptophytes). (4) Trees, i.e., woody plants, in which the apex advances, at least in the young plants, while the first side branches soon die off, or the branching can stop altogether during the first years. This produces a trunk, which later develops a crown through extensive branching of the remaining side branches. (5) In shrubs, on the other hand, the basal buds advance; they soon develop and outgrow the original main stem.

METAMORPHOSES

Apart from the variability in external appearance, which is determined by the various branching and symmetry conditions, the variability in the

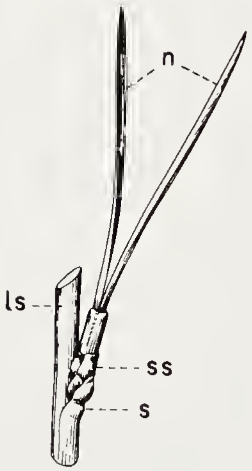

FIG. 6.16. Long and short shoots of the pine. s, Scale; ss, short shoot; ls, part of a long shoot; n, needle "leaf" (modified stem). (After Troll, modified.)

shape of the stem is further increased by morphological transformations which have to be regarded as adaptations to the external conditions, i.e., to the environment. Thus, xerophytes are adapted to extremely dry climates, hygrophytes to very wet locations, hydrophytes to aquatic life, tropophytes to locations with periodically changing moisture conditions, halophytes to saline soils, etc. These changes, which are known as metamorphoses, can be so thorough that the morphological character of the organ concerned can only be ascertained by exact morphological and anatomical study. A given basic organ, e.g., the stem, can assume the appearance of another organ, such as a leaf, as is the case in the phylloclades (see below). In spite of their external similarity, phylloclades and leaves are only analogous and, in spite of the external differences, the stem and phylloclades are homologous, i.e., they can be traced back to the same basic organ. Some of the most important stem metamorphoses are reproduced in Fig. 6.17.

Adaptation to extremely dry locations, e.g., in the desert and steppe regions, leads to very characteristic, so-called xeromorphic transformations of the stem (and also of the other basic organs, see the next chapter). Succulence should be mentioned in the first place; this term describes the formation of juicy sappy water reserve tissues. In stem succulents the reserve tissues are formed from the shoot, e.g., from the primary cortex; this is the case in cacti. Comparison of the two halves of Fig. 6.17A shows how the strongly succulent form can be derived from the stem. The subtending leaves and side shoots are only slightly developed, and the leaves of the side shoots are transformed into thorns. Assimilation is taken over by the stem itself. Apart from the cacti (Cactaceae) stem-succulent forms occur also in the spurge (Euphorbiaceae), the composite family (Compositae), and other groups. This similarity in external shape in the representatives of different systematic groups, brought about by adaptation to similar external conditions, is known as *convergence.* Reduction of the leaves, apparent already in the stem succulents, leads in other plants to a leaflike flattening of the short stems (phylloclades) or even of the long shoots (cladodes). The leaflike structures of the phylloclades are actually side shoots, as shown by the fact that they are situated in the axils of subtending leaves and carry small scale-shaped leaves themselves, in the axils of which flowers develop (*Ruscus*, Fig. 6.17B).

A further example of xeromorphic transformation is the strong development of sclerenchymatous tissues which impart the necessary rigidity to the plant body even when the turgor pressure is reduced due to excessive loss of water. The transformation of axillary shoots to thorns is one example; it also occurs in plants that are not distinctly xeramorphic (Fig. 6.17C). They are clearly homologous with axillary shoots as shown by

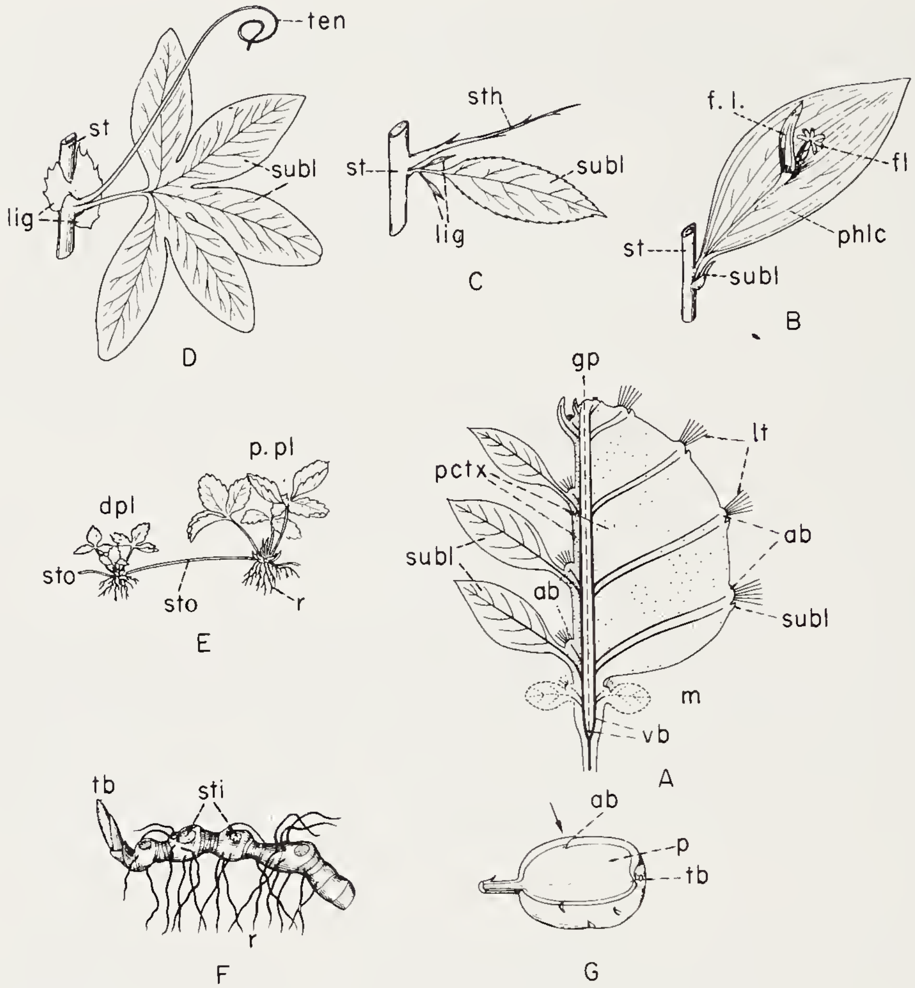

FIG. 6.17. Shoot metamorphoses. (A) Schematic derivation of a succulent stem (right) from a leafy cactus (left); (B) phylloclade of *Ruscus hypoglossum*; (C) stem thorn of *Crataegus* (hawthorn); (D) tendril of *Passiflora* (passion flower); (E) stolon formation in *Fragaria* (strawberry); (F) rhizome of *Polygonatum multiflorum* (Solomon's seal); (G) tuber of *Solanum tuberosum* (potato) with a quarter cut away. ab, Axillary bud; lt, leaf thorn; fl, flower; tb, terminal bud; m, mesoderm; vb, vascular bundle; f.l., foliar leaf; p (medulla) pith; p.pl, parent plant; sti, stigma; lig, ligule; phlc, phylloclade; pctx, primary cortex; sth, stem thorn; st, stem; ten, tendril; sto, stolons; subl, subtending leaf; dpl, daughter plant; gp, growing point; r, root. (After Troll, Wettstein, Strasburger, Miehe, and Rauh, modified.)

their positions in the axils of the subtending leaves. The thorns must not be confused with prickles (roses) which are growths of the epidermis and the underlying tissue layers.

Some climbers possess tendrils. These are formed by the transformation of the sympodial main shoot in vine (*Vitis vinifera*) and from the unbranched side shoot in the passion flower (*Passiflora*) (Fig. 6.17D).

The adaptation of plants to seasonal climatic changes also results in stem metamorphoses; this enables the plants to survive seasons which are unfavorable for growth. One example is offered by the rhizome. This is a hypogeous (mostly horizontally developing) thickened stem carrying adventitious roots. In each growing season it develops an aerial shoot which breaks through the soil surface and later dies off, while an underground growing point continues the horizontal growth. In *Polygonatum multiflorum*, the main stem comes above the surface while the axillary shoot continues to grow underground; this results in a sympodial rhizome structure (Fig. 6.17F). There are, however, monopodially branched rhizomes, too. The stem character of the rhizome can be ascertained unequivocally from morphological and anatomical characteristics, such as the lack of a rootcap, development of buds, the presence of scales, or the lack of radial vascular bundles.

Finally, the tubers must also be mentioned. These are formed either from the hypocotyl (radish, beet root) from epigeous (kohlrabi) or from hypogeous (potato) stem sections and can extend over several internodes. Underground tubers, as in the potato, can be distinguished from the rhizomes by their limited growth and also by the lack of adventitious roots. They occur as local swellings, generally in the terminal position, on the approximately horizontally growing stolons (Fig. 6.17G). The so-called "eyes" are axillary shoots located in the axils of scalelike subtending leaves, and develop into aerial shoots in the next growing season. Each plant develops several tubers, so that the tuber development is in this case connected with reproduction.

The latter holds also for many plants which develop epigeous stolons like the strawberry (*Fragaria vesca*). The growth of these is also plagiotropic (Fig. 6.17E) in the soil. Finally, they turn upright at the ends, forming an orthotropic stem and develop roots. The development of stolons is steadily repeated, and the old stolons usually die off after the daughter plants have produced roots; this, therefore, also leads to reproduction.

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Chapter 7

The Leaf

As has already been shown in a previous chapter, the leaf primordia in monocotyledons develop from swollen excrescences of the first tunica layer, i.e., exogenously (Figs. 5.19 and 6.1B). In the gymnosperms and dicotyledons the division initiating leaf primordia usually occurs in the second or third "layer" of cells near the base of the peripheral meristem (Fig. 6.1B). Periclinal divisions add cells toward the periphery and are responsible for the lateral protrusion commonly referred to as the leaf buttress.

Subsequent growth of the leaf is by the activity of three meristems—terminal, marginal, and plate. A small peg of tissue arises from the leaf buttress through the activity of a *terminal meristem* of one or several apical initials. This peglike structure grows to around 100–150 μ in height, essentially as the midrib of a leaf without a blade. Then two meristematic bands of cells on each side of the primordium, the so-called *marginal meristem*, divides in several patterns to form a lateral protuberance on each side which establishes the thickness of the presumptive leaf blade. Usually the marginal initials divide *anticlinally* to produce the protoderm, but in some cases later *periclinal* division of the marginal initials produces uniseriate protoderm cells. The submarginal initials of the marginal meristem produce cell derivatives which become the mesophyll and the vascular tissue. Finally, the *plate meristem* increases the surface area of the leaf by dividing only anticlinally with reference to the surface of the leaf blade.

In contrast to the shoot, leaves grow at their tip (acropetal growth) for only a limited time. The growth of the tip terminates very early and is replaced by growth of the intercalary or basal meristems. That is, the apex matures before the leaf base so maturation is basipetal. In monocotyledons, in particular, leaf growth is localized at the bases of leaf blade and sheath and this basal growing zone is referred to as the *intercalary meristem*. The leaves of many ferns are exceptional in that they grow steadily and acropetally from one or several apical cells. The delicate sensitive tips of their leaves are rolled up and are therefore protected by the older leaf tissue.

The first externally visible differentiation of the leaf protuberances consists of a constriction. This divides the leaf primordium into the lower and the upper part (Fig. 7.1B). The former is wider and proximal (i.e., faces the shoot) while the latter is narrower and distal. In the course of further development into a typical foliage leaf, the lower part of the leaf pri-

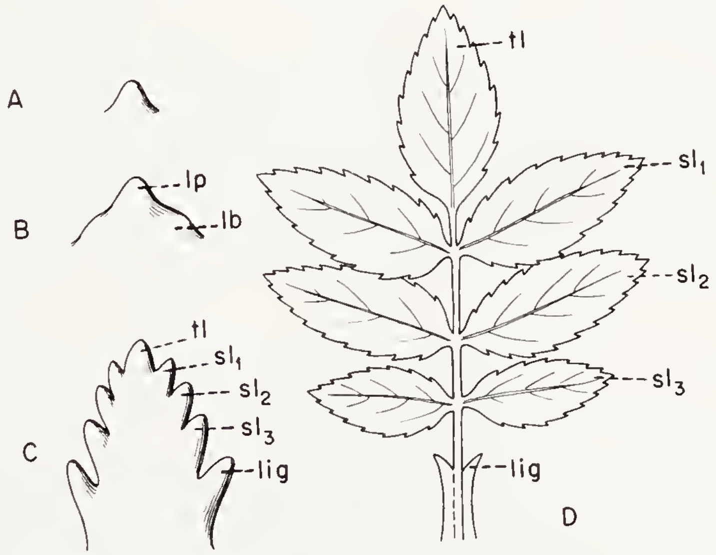

FIG. 7.1. Development of the leaflets (pinnae) in the rose. (A) Protuberance on the flanks of the growing point associated with leaf initiation; (B) articulation of the leaf primordium and leaf buttress; (C) pinna primordia resulting from activity of a terminal meristem; (D) complete leaf. tl, Terminal leaflet; lig, ligule; lp, leaf primordium; sl_1–sl_3, side leaflets, in D the marginal and plate meristems have produced a characteristic leaf blade; and lb, leaf buttress, lower part of leaf primordium. (After Troll and Stocker.)

mordium gives rise to the often flattened leafbase and occasionally the ligula (stipule), while the upper part gives rise to the leaf blades (lamina) by growth in area, width, and thickness, the latter being only moderate. The petiole also develops from the upper part, unless the leaf is stalkless (sessile); the petiole is inserted between the leaf base and the lamina by means of intercalary growth. The lamina may be disarticulated, as in the case under consideration (Fig. 7.1D) and the pinnae are then formed from the start of the development of the lamina by the marginal meristem exhibiting nonuniform activity.

Arrangement of the Leaves on the Shoot

Considerable differences exist between individual plant species with respect to the position of the leaves on the shoot and also in regard to their outer and inner appearance.

PHYLLOTAXIS

The arrangement of the leaves on the shoot can be classified into basically three types. (1) Several leaves may develop from one node, which gives rise to a so-called *whorl* of leaves at each node. These whorls obey two rules: the angle between the leaves of a whorl is constant (equidistant); and, second, the leaves in consecutive whorls are located above the gap in the previous whorl (alternation). The leaves of every second whorl are therefore placed on a vertical line parallel to the axis. These straight lines are known as orthostichies. The arrangement of leaves on a shoot which has two opposite leaves on each node is, according to the rules referred to above, *decussate;* there are, therefore, altogether four orthostichies (Fig. 7.2A). The decussate type is a variation of the whorled arrangement. (2) The arrangement of the leaves is said to be *alternate* or *helical* if there is only one leaf at each node. The number of orthostichies here depends on the angle enclosed by two consecutive leaves (angle of divergence) (Fig. 7.3). (3) When this angle is 180°, as is the case in many monocotyledons, consecutive leaves are placed exactly opposite each other. This two-ranked leaf arrangement is known as *distichous.* Other types of arrangements are produced by angles smaller than 180° (Fig. 7.2B). They are by no means random, the leaves being positioned on a spiral along the shoot. Connecting the tips of successive leaves with a line and projecting this line onto a plane yields so-called genetic spirals, which can be

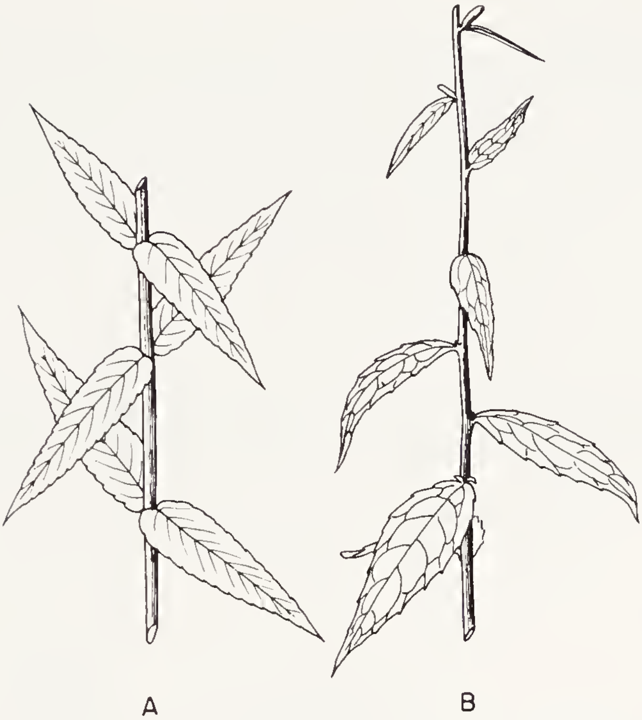

FIG. 7.2. Leaf arrangement. (A) Decussate (*Stachys palustris*); (B) alternate (*Campanula rapunculoides*). (After Frank and Miehe and Mevius.)

right- or left-handed. A very instructive example of this is the shoot rosette of the plantain (*Plantago media*, Fig. 7.3). The angle of divergence of an alternate leaf arrangement can be calculated as follows: Starting with a given leaf, estimate the number of full turns to arrive at a leaf which is exactly above the original one, i.e., belonging to the same ortho-

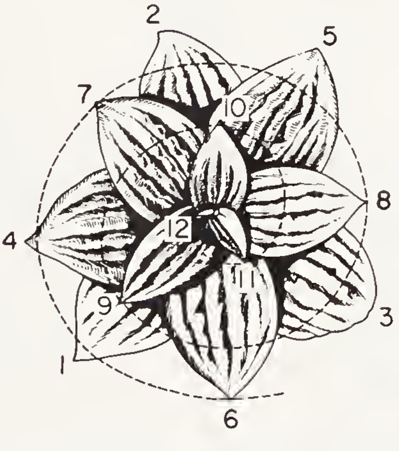

FIG. 7.3. Shoot rosette of *Plantago media* (plantain) seen in top view. The line joining the leaf tips, starting at leaf No. 6 is the genetic spiral. The leaves are numbered in the order of their emergence. [After Troll (1959, p. 60).]

stichy. In the present case the number of turns is three (Fig. 7.3). This number is multiplied by 360° and divided by the number of leaves passed along the turns (here eight). The angle of divergence is thus 135°, and the leaf arrangement is called 3/8. Other leaf arrangements are 1/3, 2/5, etc., in the Fibonacci series. These arrangements are not, however, strictly adhered to. In many cases the leaf arrangement on the same shoot changes in the course of ontogenetic development.

LEAF SEQUENCE

The first leaves developing on the shoot are the seed leaves or *cotyledons*. Monocotyledons possess only one, dicotyledons have two, while gymno-

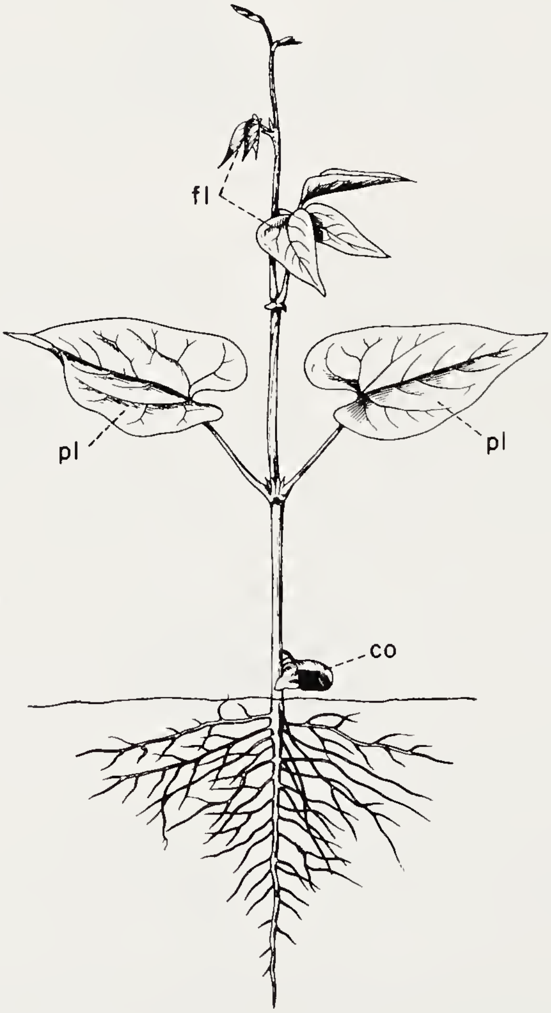

FIG. 7.4. Seedling of *Phaseolus multiflorus*. co, Cotyledon; fl, metaphyll, true foliage leaves; pl, primary leaf. [After Troll (1959, p. 42).]

sperms often have several. The latter are therefore often polycotyledonous. The cotyledons are present already on the embryo. Epigeous and hypogeous germination can be distinguished according to whether the cotyledons emerge above ground together with the young seedling or whether they remain in the soil in the seed (Fig. 7.4). The cotyledons are usually more simply built than the foliar leaves and normally are cast off or die off early.

The cotyledons are followed by foliage leaves which are often all alike. It also happens, however, that the first foliage leaves, the primary leaves, are of different (often simpler) shape than the subsequent leaves (Fig. 7.4). The subsequent leaves on the individual shoot sections may also differ (Fig. 7.5A); this is known as *heterophylly*. The leaves on a single node may differ in size (Fig. 7.5B), a phenomenon described as *anisophylly*. Anisophylly is usually a consequence of dorsiventrality.

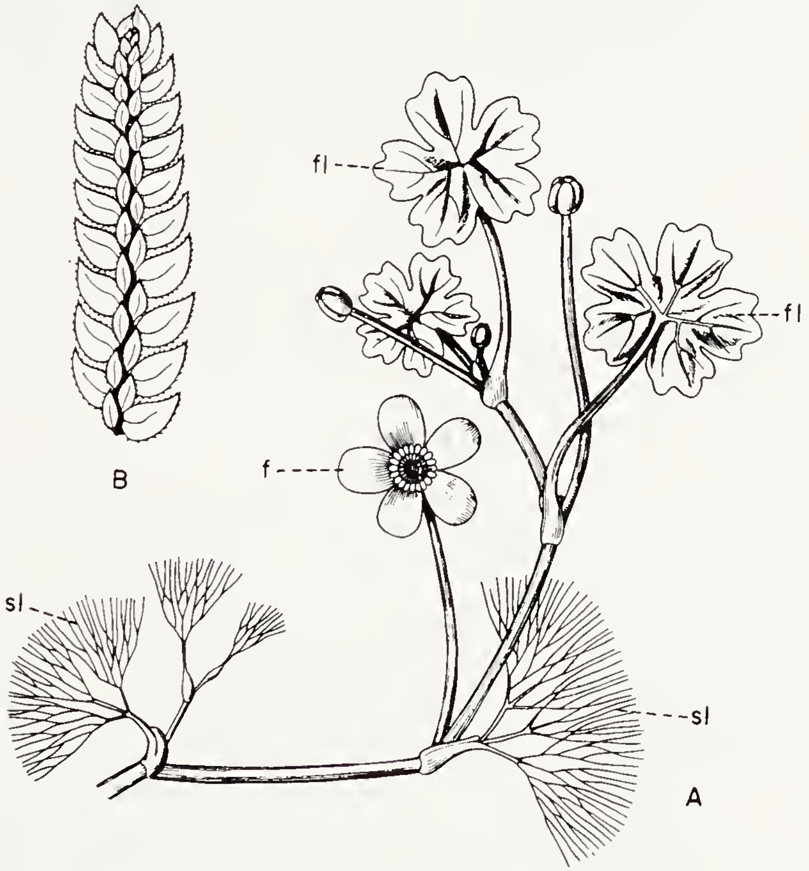

Fig. 7.5. (A) Heterophylly in *Ranunculus aquatilis* (water crowfoot). fl, Floating leaves; sl, submerged leaves; f, flower. (B) Anisophylly in *Selaginella caespitosa*. [After Troll (1959, p. 689).]

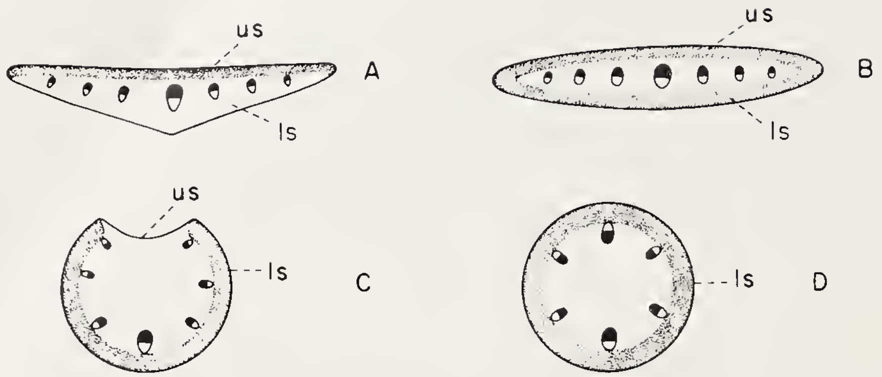

FIG. 7.6. Schematic leaf types in cross section. (A) Bifacial; (B) equifacial; (C) transition to the unifacial leaf; (D) unifacial. Assimilation parenchyma shown dotted. us, Upper surface; ls, lower surface. [After Rauh (1950, p. 81).]

In the majority of cases the foliage leaves are dorsiventral, i.e., the upper and lower sides are not identical (Fig. 7.6A). Such leaves are also known as bifacial, leaves identical on both sides being called equifacial (Fig. 7.6B). In unifacial leaves, common in many monocotyledons, the upper sides are undeveloped, and the whole leaf surface develops from the morphological lower side (Fig. 7.6C,D).

Apart from the foliage leaves proper, the stem often carries leaves of simpler shape, frequently only scalelike and covered with hyaline membranes. These are described as cataphylls when they precede the development of foliar leaves and as bracts or epiphylls when they occur beyond the region of foliar leaves. The former occur on rhizomes and the latter mainly in the region of the flowers, where they represent the transition from foliage leaves to petals (see p. 279).

Anatomy of the Foliage Leaf

The dorsiventrality of the bifacial leaves manifests itself in their anatomy (Fig. 7.7). The leaf is covered on both sides by an epidermis, with a cuticle and usually devoid of chloroplasts. The leaf tissue or mesophyll lies between the two epidermal layers. The mesophyll consists of the palisade parenchyma on the upper side and the spongy parenchyma underneath. The palisade cells are slightly elongated and lie perpendicular to the leaf surface. They are fairly close packed, contain numerous chloroplasts (see p. 50), and therefore represent true photosynthetic tissue. The palisade parenchyma can be in one or two layers. The cells of the spongy parenchyma contain fewer chloroplasts, are irregular shaped

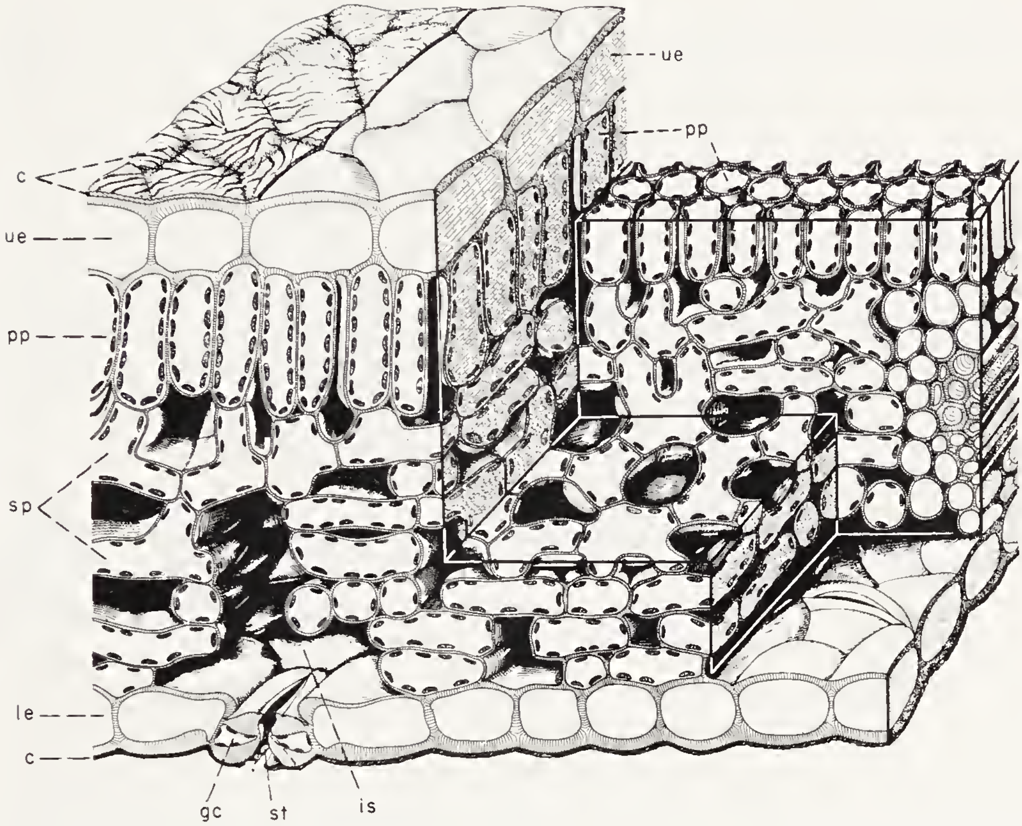

Fig. 7.7. Structure of the leaf of *Helleborus niger* (black hellebore, Christmas rose). is, Intercellular spaces; c, cuticle; ue, upper epidermis; pp, palisade parenchyma; sp, spongy parenchyma; gc, guard cell; le, lower epidermis layer; st, stoma, opening between guard cells. [After Mägdefrau (1951).]

and are separated by large intercellular spaces. The intercellular system is connected with the atmosphere through pores (stomata) in the epidermis and brings about the exchange of gases and the release of water vapor. In hypostomatic leaves the stomata are restricted to the lower side of the leaf, while in amphistomatic ones they are distributed over both sides. The case of the epistomatic floating leaves is a special one: The lower sides of these are resting on the water and the stomata are therefore on the upper side. Most leaves are simpler than *Helleborus* (Fig. 7.7) having a cuticle on only the upper epidermis and not having recessed guard cells with inner and outer stomatal chambers as illustrated here.

Structure of the Stomatal Apparatus

The stomata are formed by late division from the epidermal cells during leaf expansion. Various processes of stoma differentiation are encountered.

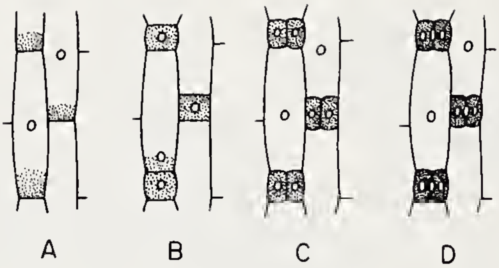

Fig. 7.8. Development of the stomata in *Iris.* (A) and (B) Unequal division of an epidermal cell, the smaller becoming the mother guard cell; (C) division of the mother guard cell to form two guard cells; (D) stoma forms as guard cells round off and pull apart. (After Popham from "Textbook of Botany for Colleges.")

The present discussion will be limited to the most common so-called amaryllid-type which occurs in many monocotyledons and dicotyledons. In this case the mother cell of the guard cells (Fig. 7.8A,B) develops by the unequal division of an epidermis cell. The mother cell then divides longitudinally to form the two guard cells (Fig. 7.8C), which round off and pull apart to form a cleft (stoma) in the middle of their common cell wall (Fig. 7.8D).

The complete stomatal apparatus, an example of which is shown in Fig. 7.9, consists of two approximately bean-shaped guard cells, which come into contact only at their ends and exhibit the opening or stoma in the middle. The narrowest part of this is known as the central opening, which widens outward and inward into the outer and inner chambers, respectively. The latter leads on into a relatively large cavity, called rather

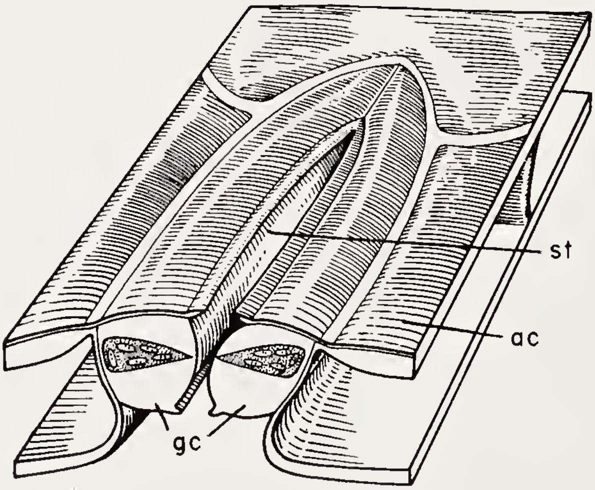

Fig. 7.9. Schematic stomatal apparatus in *Helleborus.* gc, Guard cells; ac, accessory cells; st, stoma. (After an original drawing by Dr. A. Grahle.)

inappropriately the stomatal chamber, which is connected to the intercellular system of the leaf. In many cases the guard cells are surrounded by accessory cells which also differ from the epidermis cells externally and which must be regarded as part of the stomatal apparatus. In contrast to the epidermis cells, the guard cells do bear chloroplasts. The walls of these cells are unevenly thickened. In the present case, the guard cell walls are much thickened on the side bordering the stoma, while the other walls bordering on the accessory and epidermal cells remain unthickened. The structure of the guard cells is closely connected with the function of the stomata. The thin rear wall stretches as the turgor pressure increases. The walls facing the opening are prevented from stretching by the wall thickening, so that the guard cells are pulled apart, thus opening the stoma. Conversely, a decrease in turgor leads to a slackening of the rear walls and thus of the guard cells causing the stoma to close. By means of this mechanism the plant is able to regulate the release of water vapor and also gas exchange.

ARRANGEMENT OF THE VASCULAR BUNDLES

The vascular bundles enter the leaf through the petiole as the so-called leaf trace (Fig. 6.5). They are arranged in cross section as a semicircle open at the top. In the leaf blade they branch in various ways. In most dicotyledons the vascular bundles also known as nerves or veins, form a multibranched net whose branches emerge from a relatively thick main central nerve (Fig. 7.10A). They become steadily thinner and finally terminate in the mesophyll. This arrangement allows rapid distribution of water and the salts dissolved in it over the whole leaf area. The parallel veined leaves, characteristic of the monocotyledons, contain parallel to their long axis a large number of veins of approximately equal thickness and running roughly parallel (Fig. 7.10B). Normally, the vascular bundles are collateral and are so arranged that the xylem is on the upper and the phloem on the lower side.

NEEDLE LEAVES

The needle leaves of conifers (Fig. 6.16) have a characteristic xeromorph structure differing markedly from that of the usual foliage leaf. It is represented in Fig. 7.11 by the pine. The stomata are embedded in the leaf, and the epidermal walls are so strongly thickened that the cells have only a relatively small lumen. The needle owes its great strength to the

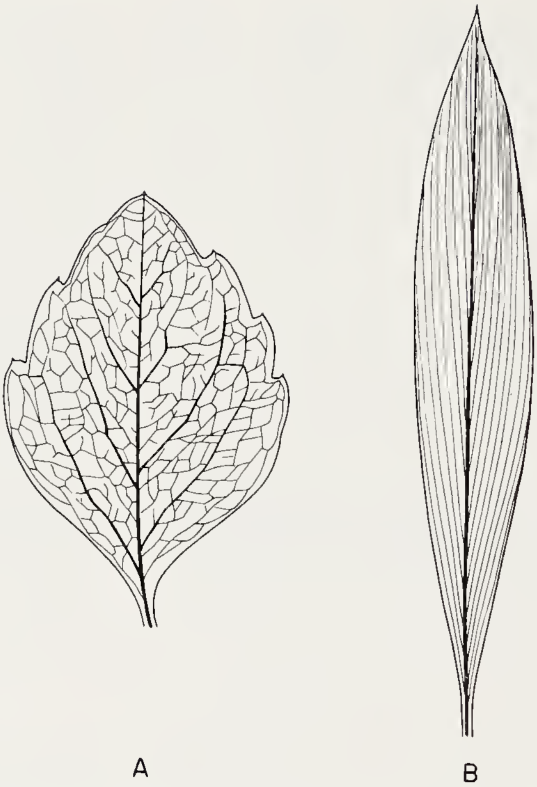

Fig. 7.10. Course of the vascular bundles in leaves: (A) networklike arrangement in *Impatiens noli tangere* (dicotyledons); (B) parallel arrangement in *Curculigo recurvata* (monocotyledons). [After Oehlkers (1956, p. 127).]

epidermis and to the hypodermal sclerenchyma tissues underneath. Only then does the assimilation parenchyma follow; the cells walls in this tissue fold inward into the lumen of the cell (plicate mesophyll). Like the shoot, the leaf tissue contains resin ducts, surrounded by a sclerenchymatous sheath (Fig. 7.11B). Along its axis the needle has a double-stranded vascular bundle which consists of two collateral bundles; these are surrounded by a special transfusion tissue. The latter consists partly of tracheidal cells and partly of cells densely cytoplasmic, and it is responsible for the exchange of water and other materials with the surrounding leaf tissue.

Many investigators consider the needle leaves to be modified (short) shoots.

Metamorphoses of the Leaf

As we have seen, the shape of the typical leaf is flat, corresponding to its function as an organ of photosynthesis and transpiration. It does not

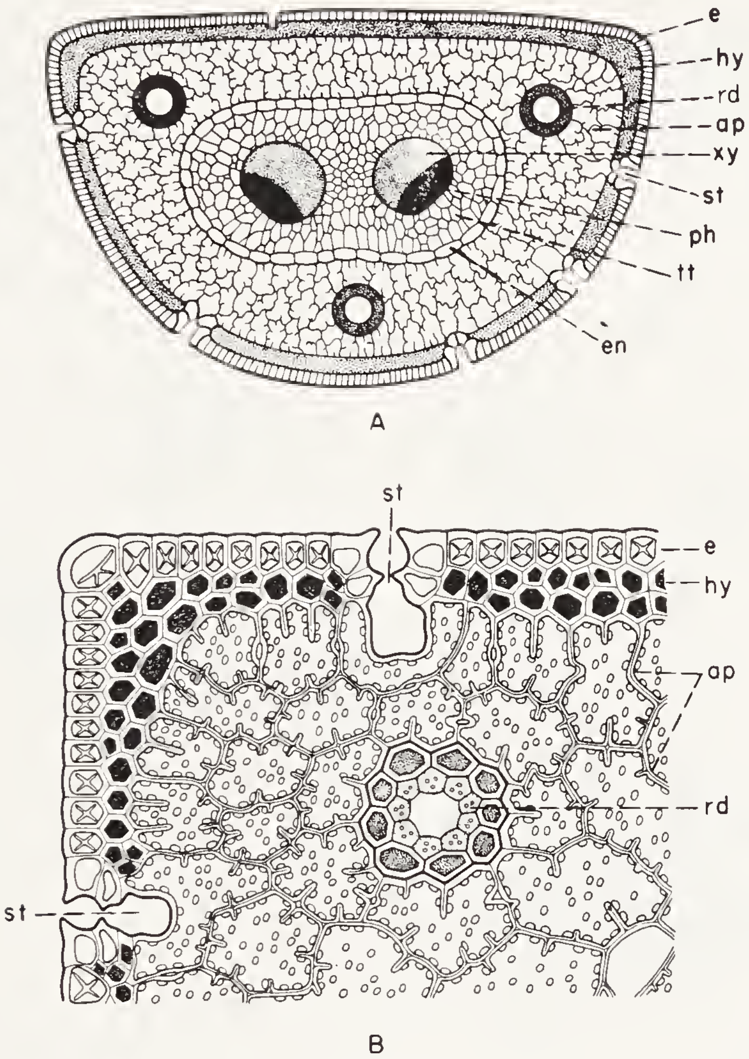

Fig. 7.11. Structure of a pine needle (*Pinus sylvestris*). (A) Overall view of the cross section (schematic); (B) enlarged view of part of the cross section. plm, Plicate mesophyll; e, epidermis; rd, resin duct; hy, hypodermis; ph, phloem; st, stoma; tt, transfusion tissue; xy, xylem; and en, endodermis. (After Wettstein, Kny, and Vaihinger.)

always develop an entire margined surface, but can be more or less deeply crenate or sinuate, subdivided into digital parts or pinnae, or be of some other shape. However, its structure is always the characteristic foliage leaf structure as discussed above.

As in the case of the stem, there are numerous cases in which both the outer appearance and the anatomy of the organ suffer such thorough transformation that the leaves are no longer easily recognizable as such. These are therefore leaf metamorphoses, a few examples of which are shown in Fig. 7.12. The most extreme case, i.e., the total lack of development of the leaf blades and the takeover of their functions by the stem, has already been discussed in the previous chapter (Fig. 6.17A,B). The lack of development is not quite so pronounced in the phyllodia (Fig. 7.12A). As is shown by the transitional forms of *Acacia*, here it is only

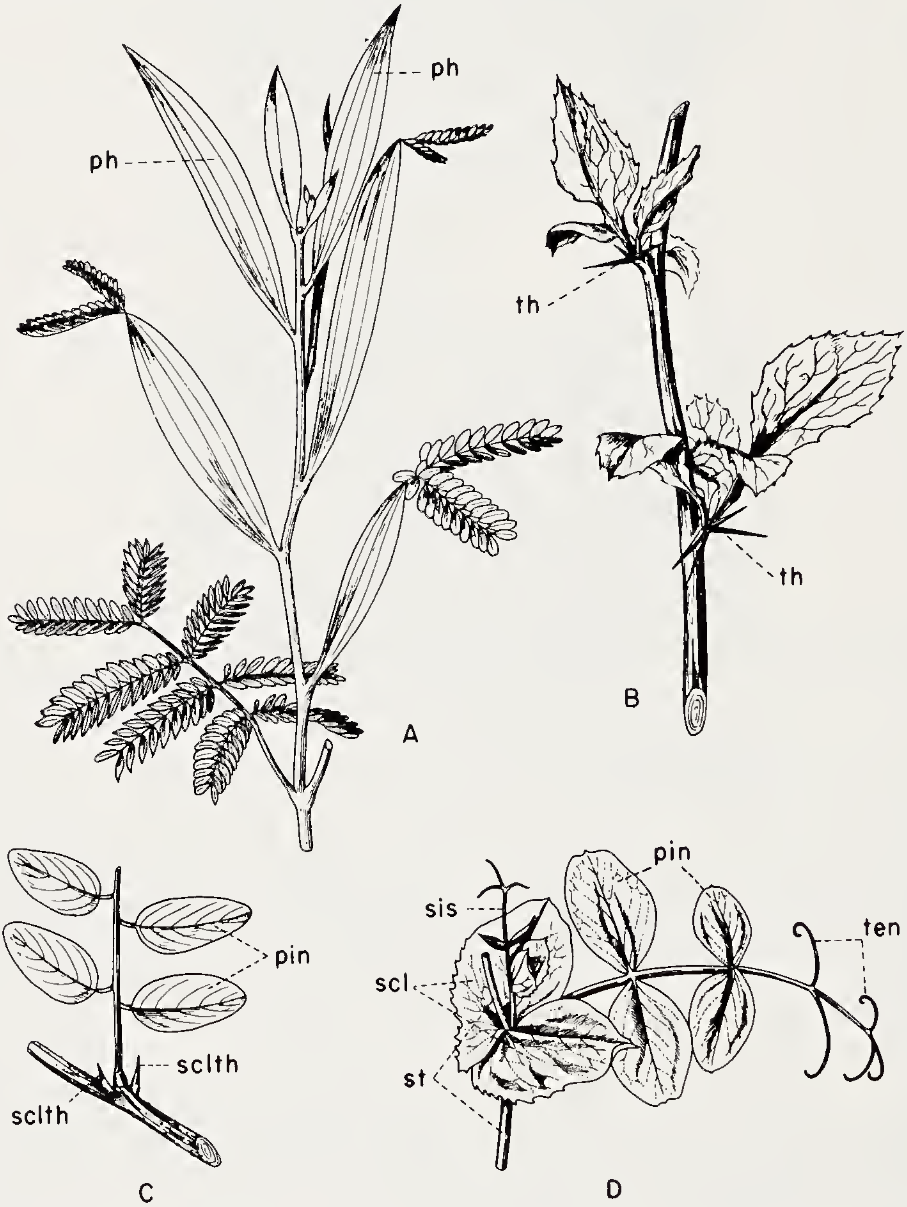

Fig. 7.12. Leaf metamorphoses. (A) Phyllodia of *Acacia heterophylla*. Transitions from pinnati-partite foliage leaves (below) to the phyllodia (above); (B) leaf thorns of *Berberis vulgaris* (barberry); (C) scale leaf thorns of *Robinia pseudo-acacia* (false acacia); (D) leaf tendrils of *Pisum sativum* (pea). th, Leaf thorns; pin, pinna; ten, tendrils; scl, scale leaf; sclth, scale leaf thorn; ph, phyllodia; st, stem axis; sis, side shoot. [(A) After Reinke, (D) after Troll.]

the leaf blades that are reduced, while the petioles undergo leaflike widening and take over the functions of the petiole. In the pitcher plants (*Nepenthes*) the leaf base is developed like an assimilation organ (see p. 260). Examples of xeromorphic adaptations arc the reduction in leaf area, the diminution of stomata, and the strong development of sclerenchyma elements, which has already been shown in the needle leaves (Fig. 7.11). The leaves are often transformed into thorns, as in the cacti (Fig. 6.17A), which have already been discussed, or in *Berberis vulgaris* where uni- or multiradial thorns take the place of subtending leaves (Fig. 7.12B). Here there are normal short shoots with leaves in the axils of the leaf thorns. As is shown by the example of false acacia (*Robinia pseudo-acacia*), the scale leaves can also be transformed into thorns (Fig. 7.12C). Finally, in climbers the leaves are often transformed wholly or partly into tendrils. The latter happens for instance in peas (*Pisum sativum*) (Fig. 7.12D). Here the lower part of the pinna is developed normally, while the upper part is transformed into a leaf tendril which is correspondingly pinnate.

An example of adaptation to geophytic[1] conditions is furnished by the bulbs. In onions (*Allium cepa*), the fleshy shell-shaped overlapping bulb scales develop from the leaf base of dead foliage leaves (Fig. 7.13). The stem is shortened into a small compact axis, the bulb axis, which is nearly disk-shaped and supports the leaves. In the axils of the bulb scales there are axillary buds which start to grow at the beginning of the new growing season, making use of the reserve substances stored in the scales. In other cases the bulbs are formed from cataphylls.

Finally, it can be pointed out that there are many leaf succulents in which the water-storage tissues occur in the leaves. Some further examples of leaf metamorphoses will be discussed under the heading of insectivores (see p. 257).

Summary

In summary, the leaf is a plant organ modified for transpiration and photosynthesis. The hundreds of stomata per square millimeter on the leaf blade give off water vapor. Since the vascular system of the leaf is continuous with that of the stem and root, transpiration pull is mainly responsible for the movement of water in xylem elements to the leaf where it is needed for photosynthesis The leaf is variously modified to cut

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[1] Geophytes are perennial plants which winter exclusively with hypogeous organs, while all the epigeous parts die off (perennial herbs, see p. 150).

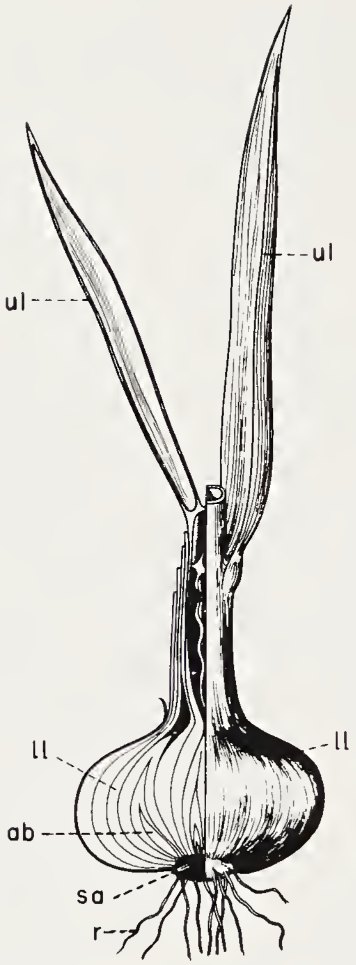

FIG. 7.13. Onion (*Allium cepa*): left, cross section; right, surface view. sa, Stem axis; ab, axillary bud; ul, upper part of leaf; ll, lower part of scale leaf; r, root. [After Rauh (1950, p. 39).]

down water loss: Cuticle, guard cells, sunken stomata, hairs on surface to cut evaporation, etc.; but water loss is a necessary evil. The leaf is also modified for photosynthesis. Leaves are arranged on the stem (phyllotaxis) in such a way that they do not shade each other; the broad, flat, thin blade will intercept and absorb a maximum of light into the chloroplasts of mesophyll cells. The stomata permit entrance of carbon dioxide which goes into solution in the water films on the cells walls and then enters the cells to be used in photosynthesis. The stomata also permit the release of oxygen on which all animal life depends.

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Chapter 8

The Root

The third basic organ of the Tracheophytes, the root, differs from the stem mainly in that it never bears leaves. Like the stem it grows by means of a growing point (Figs. 5.19 and 8.1), but this is enclosed by the root cap, unlike the stem tip which is enclosed by bud scales. The tip of the root is occupied by the embryonic zone, also known as the zone of cell division. This definition is, however, incorrect, partly because the so-called dormant center [(cf. p. 126) whose cells seldom if ever divide] lies in the apical region of this zone, and partly because the process of cell division continues far into the neighboring elongation zone. It is also remarkable that the regions of most active cell division in the various tissue systems of the root (central cylinder, cortex, rhizodermis, pericycle) are found not at equal heights but at various distances from the apex.

Cell elongation is connected with the formation of vacuoles (see p. 73). In contrast to the stem, the elongation of the root is restricted exclusively to the elongation zone beginning at 1.5–2 mm behind the root tip. The elongation zone, which is usually some millimeters long, merges without a sharp boundary into the root hair region (Fig. 8.1).

The Primary Structure of the Root

The differentiation processes occur in the zone of the root hairs. Formation of root hairs is only one of these processes, although the only externally visible one. The root hairs grow likewise by unipolar apical growth (see p. 91), and can emerge from any epidermal cell not strongly polar (Fig. 8.1); however, the so-called trichoblasts cells arise from unequal divisions of strongly polar epidermis cells similar to the formation of guard cells, and of the two daughter cells the small, densely cytoplasmic trichoblast cells alone are capable of developing root hairs.

RHIZODERMIS

In contrast to the epidermis cells of the stem, the walls of the root hairs are not thickened, cutinized, or covered by a cuticle. This is connected with their function, which is the uptake of water and salts; this task is also greatly facilitated by the structure of the cell wall and also by the increase of the root surface brought about by the development of root hairs. Owing to these peculiarities in the anatomy and function of the root epidermis, it is also known as rhizodermis to distinguish it from the stem epidermis. The root hairs can in any case be missing as in aquatic and marsh plants.

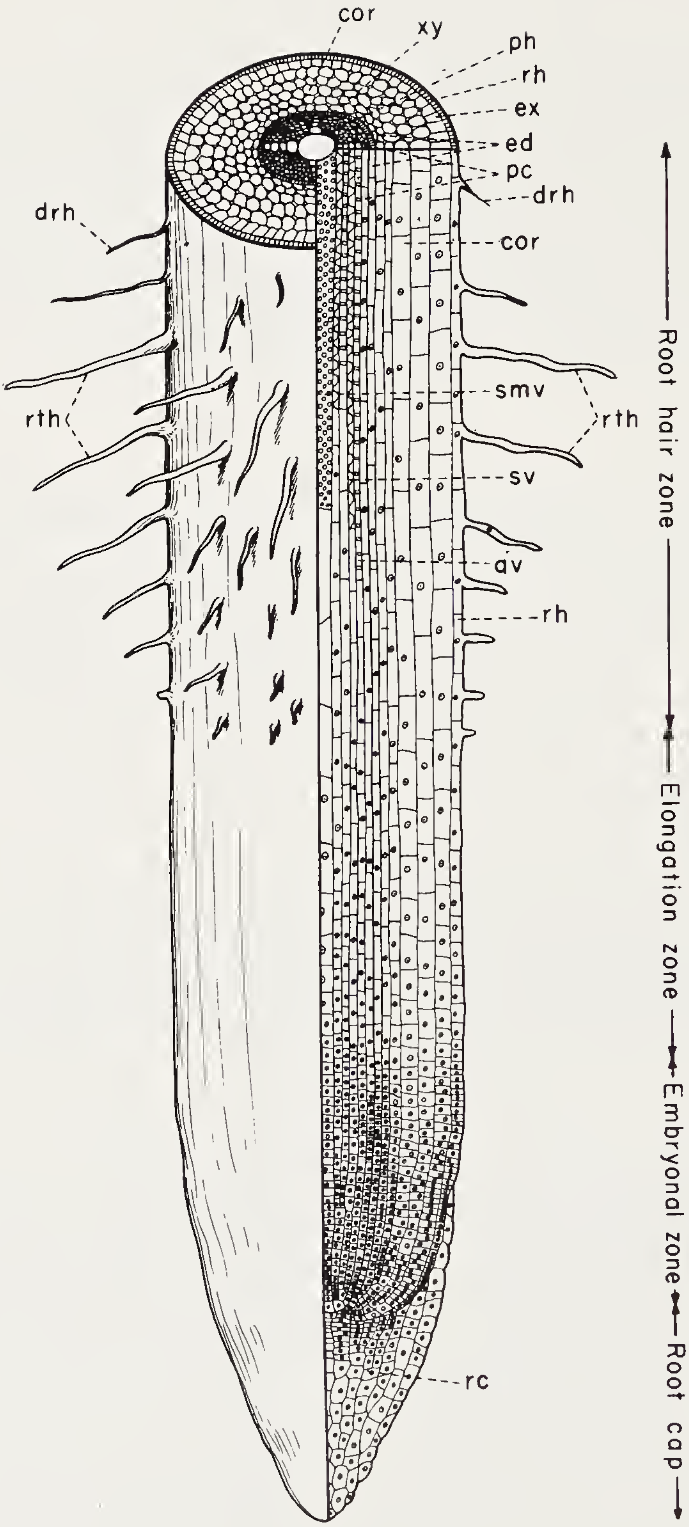
The life-span of root hairs is mostly restricted to a few days. They grow to a length of some millimeters in this time, and penetrate between the soil particles with their slightly gelatinized cell walls (Fig. 9.3). They are then put out of action and die off, starting from the rear end or oldest part of the root (Fig. 8.1). The rhizodermal cells die off with them, and the root must therefore develop a new tegumental tissue, the exodermis.

EXODERMIS

The exodermis develops from the subrhizodermal layer, sometimes from several layers of the cortex. Its complex of long and short cells remain mostly alive due to the limited extent of cork deposition. Some of the short thick-walled exodermal cells are completely without suberin for some time, so that the uptake of water and salts is possible to some extent even beyond the root hair zone.

CORTEX AND CENTRAL CYLINDER

Differentiation of the other root tissues occurs simultaneously with the development of root hairs; this differentiation is most pronounced in the


cor
xy
ph
rh
ex
ed
pc
drh
drh
cor
rth
smv
rth
sv
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rh
rc
Root hair zone
Elongation zone
Embryonal zone
Root cap

cortex and in the central cylinder. The cortical cells are parenchymatous, normally free from chlorophyll (only in the aerial roots can they contain chloroplasts), and serve as storage tissues, mainly in the older parts of the root. The innermost cortical layer, the *endodermis*, functions as a physiological sheath and controls the passage of water and salts dissolved in it into the central cylinder (Fig. 8.1). The characteristic structure (Casparian strips or secondary thickening) of their cell walls has already been described in Chapter 4 (Fig. 4.18). Here, too, we may find unaltered transfusion cells, which always lie above the xylem rays.

The central clyinder contains the vessels and sieve elements which are arranged in alternating radial vascular bundles (Fig. 8.1). Differentiation of the vessels (protoxylem and metaxylem) can be observed on a section parallel to the root axis. In the center, the xylem may converge directly (Fig. 8.1); alternatively, the center can be occupied by strands of sclerenchymatous or parenchymatous cells (Fig. 8.3) so that the xylem is restricted to radial vascular bundles. The arrangement of the reinforcing elements in the center is in accordance with the tensile strain to which the roots are subjected. The phloem strands lie between the radial files of xylem. The outermost cell layer, bordering on the endodermis, is known as the *pericycle*.

BRANCH ROOTS

While the primary root of seedlings is at first unbranched, the continued expansion of the above ground parts of the plant is accompanied by branching of the root. This branching occurs exclusively sideways, with the exception of the roots of the Lycopodineae which branch dichotomously. In contrast to the axillary shoots, the side roots develop endogenously, from the pericycle in the gymnosperms and angiosperms and from the innermost cortex layer in the pteridophytes. They develop either above the radial xylem bands or above the parenchyma plates which separate the xylem from the phloem. They are therefore arranged above each other in columns whose number is equal to or is twice the number of the xylem bundles. The side roots develop endogenously, and they must therefore break through the cortical layers; this they do by

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FIG. 8.1. Schematic anatomy of a root tip: left, face view; right, vertical section; top, cross section. drh, Dead root hairs; ed, endodermis; ex, exodermis; rc, root cap (calyptra); pc, pericycle; ph, phloem; av, annular protoxylem vessels; rh, rhizodermis; cor, cortical cells; sv, spiral protoxylem vessels; smv, scalariform metaxylem vessels; rth, root hairs; and xy, xylem. (Partly after Holman and Robbins.)

pushing the cortical cells mechanically apart or breaking them down enzymatically.

In the typical case the root exhibits racemose branching, i.e., the side branches are less well developed than the main root (Fig. 8.2A). Such a root system is said to be allorhizal. The main root normally penetrates the soil perpendicularly, i.e., orthotropically, while the first-order side roots grow more or less horizontally, i.e., plagiotropically. With continuing branching, the side roots of higher order generally do not exhibit any distinct orientation. In contrast to the allorhizal root development, the root development of the pteridophytes and the monocotyledons is homorhizal. In the latter, the root tip stops functioning fairly early, the primary root dies off (Fig. 8.2B) and is replaced by numerous adventitious roots. This is known as a secondary homorhizal process. On the other hand, primary homorhizal development is exhibited by the pteridophytes.

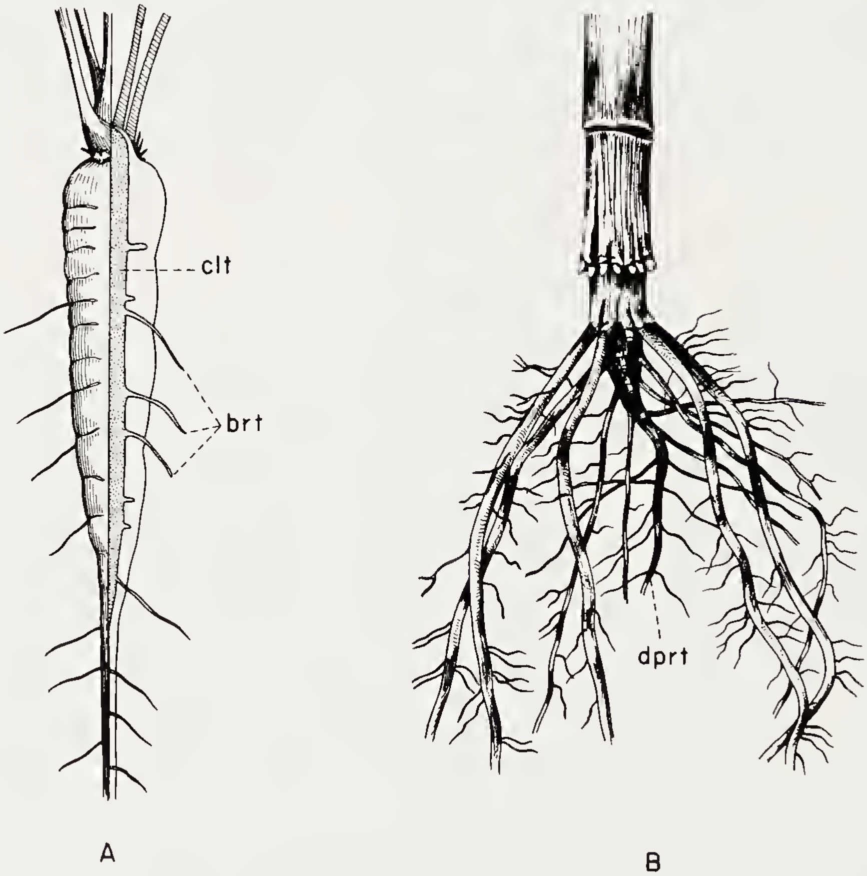

Fig. 8.2. Allorhizal (A) and homorhizal (B) root development. (A) *Daucus carota* (carrot): left, face view; right, longitudinal section. (B) Maize (*Zea mays*). dprt, Dead primary root; brt, branch roots (xylem); and clt, central lignified tissue. [After Rauh (1950, pp. 19 and 29).]

Here, the primary root itself grows sideways and is complemented by adventitious roots from the start.

Basically, adventitious roots can also develop on shoots and leaves as, for instance, on runners and stem cuttings. The development of such adventitions roots can also be induced by mechanical damage or by treatment with growth substances (see p. 343).

At the transition between the root and the stem, at the so-called root collar, the radial bundle goes into the collateral arrangement of the stem by a characteristic splitting of its phloem elements.

Secondary Growth in Thickness

The root starts to thicken approximately simultaneously with the secondary thickening of the stem. The cambium develops in the parenchymatous tissue bands which separate the xylem from the phloem. Above the xylem files it reaches the pericycle, the cells of which also become meristematic. This gives rise to a closed cambium mantle which is approximately star-shaped in cross section (Fig. 8.3A), corresponding to the structure of the radial vascular bundles, which may have 2–11 arms.

The root cambium, like that of the stem, develops secondary xylem inward and secondary phloem outward. Increased activity in the regions

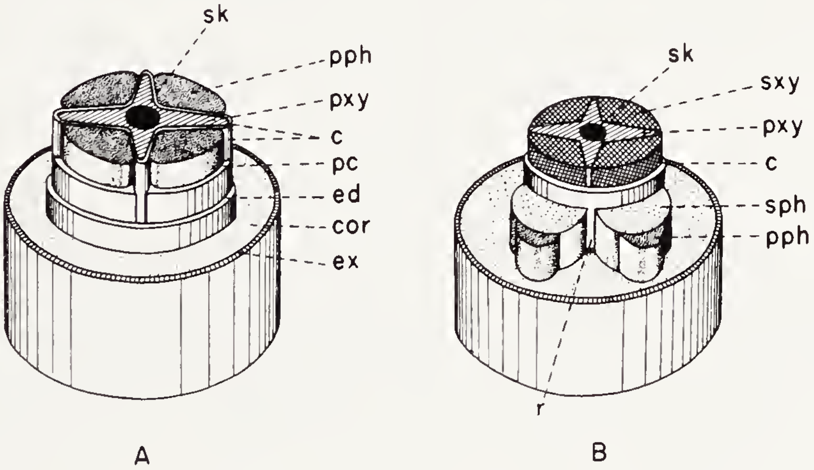

Fig. 8.3. Schematic secondary thickening growth of the root. (A) Cambium formation; (B) conditions some time after the onset of secondary thickening. c, Cambium; ed, endodermis; ex, exodermis; pc, pericycle; pph, primary phloem; pxy, primary xylem; cor, cortex; sk, sclerenchyma; sph, secondary phloem; sxy, secondary xylem; and r, ray.

lying between the xylem radii fills up the cavities with wood elements, leading finally to the formation of a central woody cylinder surrounded by a cambium mantle circular in cross section (Fig. 8.3B). The wood of the root is then very similar to that of the stem.

Phloem fibers develop behind the primary phloem strands, giving rise to wide bast bands between which medullar rays remain inserted; these lie opposite those of the wood (Fig. 8.3B). In addition, secondary medullar rays develop in the xylem and in the phloem.

Metamorphoses of the Root

Just like the stem and the leaf, the root may undergo numerous metamorphoses, which result in significant alterations in the inner and outer structure of this basic organ. There are, for instance, root succulents in which the water-reserve tissue is located in the roots, also root thorns, root tendrils, and rhizoids in root climbers [the latter in *Hedera helix* (ivy)], prop and respiratory roots in marsh plants (mangrove), and green assimilation and aerial roots in epiphytes and climbers. The root tubers can be mentioned as adaptations to geophytic conditions (see p. 167) which can be found, for example, in *Dahlia variabilis*. These can be easily distinguished from the externally similar shoot tubers by the presence of root caps, the absence of scale leaves, and by their anatomy.

Finally, mention may be made of storage roots (beets): These are strongly thickened main roots of allorhizal root systems (Fig. 8.2A). However, the hypocotyl often takes part in the constitution as well, and can under certain conditions make up the storage root by itself. Figure 8.4 shows this by way of some examples. Sugar beet is formed almost exclusively by the root (A). Secondary growth is from the regular vascular cambium but parenchyma predominates in the xylem and phloem. The turnip consists largely of the hypocotyl (B). Xylem parenchyma and pith (if present) proliferate and give rise to clusters of anomalous cambia which produce secondary vascular tissues (Hayward, 1938). The common red beet is a pure hypocotyl tuber (C) which enlarges by a series of recurrent cambia derived from pericycle and phloem, which give rise to secondary xylem and phloem cells together with storage parenchyma in broad radial bands.

In summary, the root is an organ modified and adapted to perform certain functions for the plant body as a whole. Since the area of soil occupied by the roots equals or exceeds the area of the top, the greatly branched root system firmly *anchors* the plant, the large surface area of

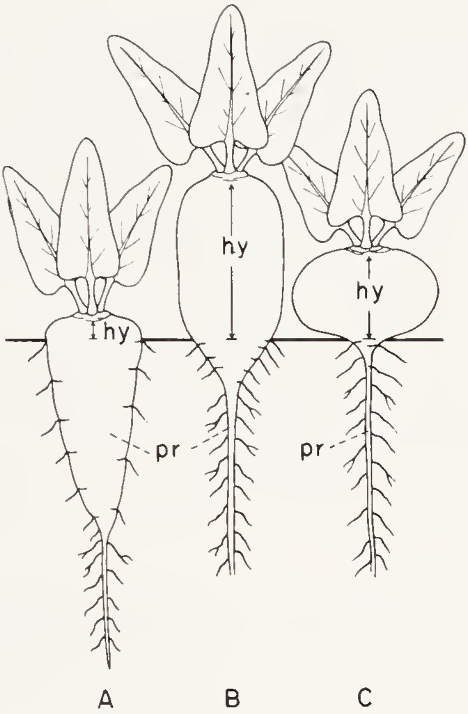

Fig. 8.4. Beet formation. (A) Sugarbeet; (B) turnip; (C) red beet. hy, Hypocotyl; pr, primary root. [After Rauh (1950, p. 118).]

branch roots augmented by the root hairs serve to *absorb* water and mineral salts from the soil solution, the well-developed vascular system *transports* materials to and from the stem and leaves, and pith, cortical, ray, and xylem and phloem parenchyma serve for *storage*.

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Chapter 9

Water and Salt Balance: Translocation of Materials

All life processes occur in the aqueous phase and, therefore, require an adequate supply of water. For this reason the water content of plants is relatively high, ranging from 60–90% and reaching 98% in many aquatic plants (Stocking, 1956). If it falls below a certain minimum value, which varies from case to case, the life processes are slowed down. Under conditions of latency (dormancy and quiescent states), the water content can drop to 5% or even less and the life processes are then barely detectable.

In the lower plants the hydration, i.e., the water status of plant cells and tissues, is generally similar to that of the environment. They are therefore restricted to locations with sufficiently high humidity, and occur either in the water itself or in very damp places. They can survive dry periods in locations of alternating humidity only in the latent condition. On the other hand, the higher plants penetrating the atmosphere must preserve their hydration against the environment, since the relative humidity of the air is seldom high enough to ensure a satisfactory course of life processes. In spite of certain protective measures, which have been described as xeromorphic adaptations, the higher plants lose water steadily to the environment, and the hydration would therefore drop below the lower tolerance limit were it not for the steady uptake of water from the soil, which usually has a higher moisture content. The plant, therefore, fits into the moisture gradient between the soil and the atmosphere, in that it takes up water from the soil, transports it upward along the path of conduction, and evaporates it again.

The uptake of mineral salts also occurs mainly through the roots. The discussion of salt metabolism has therefore been incorporated into this chapter, even though there is no causal relationship (except mass flow) between the uptake of water and of salts. Another justification for discussing this subject here is that the transport of the assimilated materials also occurs in the water transmission vessels.

The Water Balance of the Cell

As has already been stated (see p. 76), a fully grown plant cell is an osmotic system in which the cytoplasmic membrane behaves as a selectivity permeable membrane (see pp. 26, 34), while the cell wall is normally freely permeable to both water and dissolved substances. If a cell is placed in a hypotonic medium, i.e., one whose osmotic pressure is lower than that of the cell sap, water will continue to enter the vacuole until the elastic pressure of the increasingly stretched cell wall (W) becomes equal to the osmotic pressure (S_i). The cell suction pressure (S_s) depends on these two magnitudes, which can be connected by the osmotic equation of cell state

$$S_s = S_i - W$$

The variation of these three quantities can easily be followed on a graph such as Fig. 9.1. In a wholly relaxed cell the wall pressure (W) is zero, and hence the cell suction pressure corresponds to the osmotic pressure of the cell sap (S_i) (State I in Fig. 9.1). The increase in volume following an uptake of water leads to elastic stretching of the cell wall and thereby to an increase in the wall pressure, while the suction decreases accordingly (State II). Dilution of the cell sap due to the water uptake reduces the osmotic pressure to some extent. Finally, in the state of full turgescence, the wall pressure is equal to the osmotic pressure and the suction pressure is therefore zero (State III).

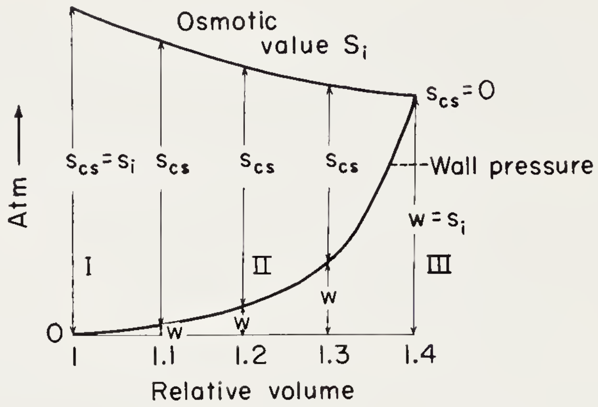

FIG. 9.1. The osmotic state diagram. S_i, Suction pressure of the cell contents (= osmotic pressure); S_{cs}, suction pressure of the cell; W, wall pressure. See text for further explanation. (After Höfler and Burstrom.)

TISSUE TENSION

The osmotically active cells may be part of a tissue, in which case the wall pressure is augmented or reduced by an additional external pressure (A); this pressure may counteract the stretching of the cell, or it may enhance it if it is negative (tension). In this case the equation has to be modified

$$S_s = S_i - (W \pm A)$$

The external pressure manifests itself in tissue tension, whose existence can be demonstrated by a simple experiment. A stem section is taken, e.g., from *Helianthus*, and a length of the pith is detached with a cork borer. The stem is then placed in water. The pith cells expand more than the cortex, and part of it will protrude at the end of the section. Inside the tissues of the stem the pith is prevented, however, from expanding fully by the vascular cylinder and cortex. The tissue tension can contribute significantly to the solidity of plant organs.

PLASMOLYSIS

If a plant cell is placed in a solution of higher osmotic pressure (hypertonic solution), water will move out of the vacuole until the osmotic pressure of the cell sap reaches that of the external solution. The decrease in cell volume connected with this loss of water leads to a relaxation of the stretched cell wall (Fig. 9.2A,B). When the wall is completely relaxed, the plasma utricle detaches itself from the cell wall on further shrinkage

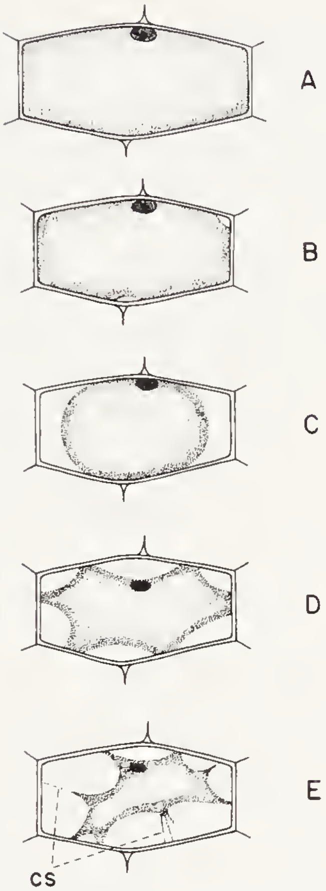

FIG. 9.2. Types of plasmolysis (schematic). (A) Turgid cell; (B) cell at the threshold of plasmolysis; (C) convex plasmolysis; (D) concave plasmolysis; (E) clumped plasmolysis. Plasma envelope (membrane + gell cytoplasm = ectoplasm) dotted area; cs, cytoplasmic strands.

(Fig. 9.2B). This process is known as *plasmolysis*. According to the strength of attachment to the wall and the consistency of the plasma, the detachment can occur smoothly and with early rounding off of the plasma utricle (convex plasmolysis, Fig. 9.2C); alternatively, if the plasma is strongly attached to the wall, rather bizarre forms can arise which are known as concave (Fig. 9.2D) or clumped plasmolysis (Fig. 9.2E) depending on the degree of distortion. Frequently the plasma is drawn out into thin threads in the process (Fig. 9.2E). The condition of the incipient separation of plasma from the cell wall is known as the plasmolysis threshold (Fig. 9.2B).

The cell remains viable in the plasmolyzed state. On transfer of such a cell into a hypotonic solution, water enters the vacuole, the plasma membrane lines up once more against the cell wall (deplasmolysis), and finally the cell becomes fully turgescent. Death of the protoplasts leads at once to loss of semipermeability, and so the ability for plasmolysis can be used as a criterion for characterizing the biological condition of the protoplasts.

The selective permeability of the plasma boundary layers is, however, not absolute (see p. 36). Over long periods of time they allow the transmission of dissolved substances too; also here we must mention *mass flow* where certain ions may be carried into or out of the cell with the mass flow of other ions although under other circumstances they might be selected against. The plasma membrane and the tonoplast can vary a great deal as regards their permeability to certain ions or molecules. The penetration of these into the protoplasm through the plasma membrane is known as intrability, while penetration through the boundary layer into the vacuole is described as permeability (Stadelmann, 1956). Ordinarily it would not be necessary to draw such a distinction and the term permeability is preferred except for active absorption. Evidence indicates that solutes and water may diffuse across the plasma membrane rather readily, but the tonoplast is highly selective so ions and water accumulate in the vacuole only under conditions of active transport or long-term accumulation by uptake of molecular aggregates or "carriers" which then dissociate in the tonoplast. Thus, if a plasmolyzed cell is left for a longer period in a hypertonic solution, the volume of the vacuole will eventually be observed to increase again, in spite of the concentration of the outer solution having remained unchanged. Apparently, therefore, ions or molecules enter the vacuole from the cytoplasm, thus raising the concentration of the cell sap.

Water Uptake

This may take place over the whole plant surface as is shown by the example of submerged aquatic plants. Basically, this is not true for the aerial parts of terrestrial plants since they have xeromorphic adaptations to prevent water loss, e.g., cuticle and cork, and seldom come into direct contact with water; hence, water uptake is practically restricted to the roots. An exception to this are some epiphytes which employ organs other than the roots for the water uptake, e.g., the bromeliad plants in which the leaf margins overlap to form a cistern for collecting rainwater; this water is then taken up by special absorption hairs on the leaves.

In the soil the water is bound in various ways. The gravitational water which percolates down to the ground water table is not available to plants as their root system usually penetrates only the upper layers of the soil. The water held in these layers occurs partly in the hydrated shells of soil colloids and partly in the capillaries of the soil. This capillary water is the main source utilized by plants. In any case, the water in the soil is not pure but is a solution of salts and a certain osmotic value, soil suction pressure, which must be overcome by the plant if it is to take up water. This pressure is normally of the order of a few atmospheres, but in extreme cases (deserts, saline steppes) it can amount up to 100 atm. Only certain specialized plants can therefore thrive on such soils.

The root hairs penetrate between the soil particles (Fig. 9.3) and thus come into contact with capillary water which they draw over long distances across the soil by the steady uptake of water. The first step in water uptake (imbibition) consists in swelling of the cell wall; in the capillary cavities of this wall (Fig. 3.13) the water transport can proceed further through the root cortex (Fig. 9.3). As the cells of the cortex and those of the central cylinder represent a water gradient between the rhizodermis and the vessels, the water can also be transmitted from cell to cell by *diffusion* (from greater to lesser concentration). The mechanism of the transfer of water from the cortical tissue to the central cylinder has not yet been clarified. In addition to diffusion it seems to involve an active process requiring expenditure of energy, which can perhaps be compared with the active secretion of gland cells. The forces developed in this process can be identified as *root pressure*. This can be directly measured manometrically if a plant is decapitated and the stump is connected to a manometer. The pressure is usually small, but in some plants it can reach 6 atm. The exudation of many trees (e.g., birch) on mechanical damage is

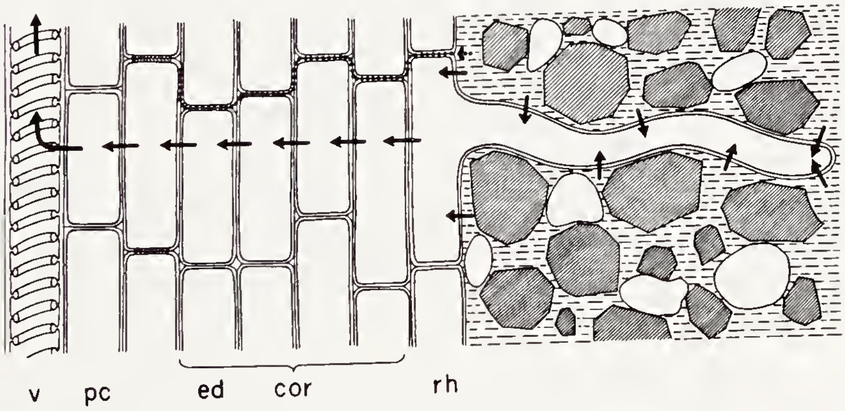

FIG. 9.3. Schematic water uptake by the root. Root hair among soil particles (hatched) and air pockets (plain). The rest of the pore space is filled with water. Arrows indicate the direction of water movement through the cells, and the broken line (free space) transport of water through the cell walls, although all walls are freely permeable. ed, Endodermis with Casparian strips; v, vessels; pc, pericycle; rh, rhizodermis; cor, cortical cells.

also due to such forces (root pressure). Still another factor is a diffusion pressure deficit or transpiration pull (see below).

Transpiration

As has already been mentioned, the above ground plant organs continuously evaporate water vapor due to the moisture gradients. This process is known as *transpiration;* a distinction is made between cuticular and stomatal transpiration.

CUTICULAR TRANSPIRATION

In this process the outer walls of the epidermis release water vapor through the cuticle and shrink at the same time (Fig. 9.4). The loss of water is made good partly by water absorption through the anticlinal walls of epidermal cells and partly from the vacuole; this increases the suction pressure of the cell which enables the epidermis cell to draw water from neighboring cells, etc. Cuticular transpiration cannot be con-

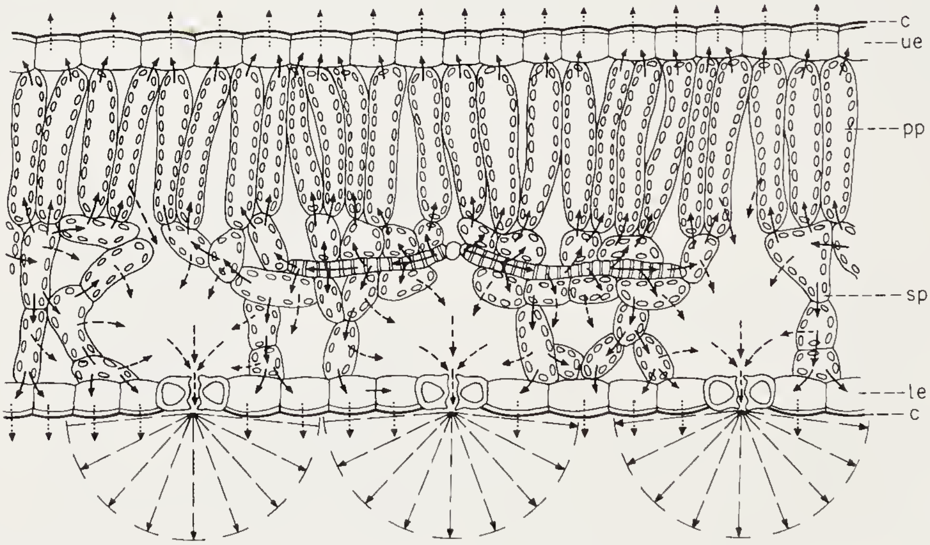

FIG. 9.4. Transpiration of a foliage leaf (schematic). In the middle of the leaf cross section there are two vessels ending in cul-de-sac. Regions of higher water vapor concentration are shown around the stomata (water vapor domes). (———>) Direction of water uptake; (- - - ->) path of evaporating water; (· · · ·>) cuticular transpiration; (— —>) stomatal transpiration; c, cuticle; ue, upper epidermis; pp, palisade parenchyma; sp, spongy parenchyma; le, lower epidermis.

trolled by the plant, and its extent depends entirely on the relative humidity of the environment. On the whole, its magnitude is small and amounts to only 5–10% of total transpiration. In individual cases this value depends, of course, on the permeability of the cuticle and the cutinized layers.

STOMATAL TRANSPIRATION

As the name implies, this process occurs through the stomata; it therefore can be controlled by the already discussed stomatal mechanism (see pp. 161–163). When the stomata are fully open, it amounts to well over 90% of the total transpiration. However, the stomata are by no means always fully open, their degree of opening depending on external conditions, especially, light, atmospheric humidity, and temperature (sec p. 389). A typical daily course is represented in Fig. 9.5. Transpiration increases continuously during the morning, reaches a maximum around midday, and decreases during the afternoon. On hot and dry days the amount of water vapor lost may be high, and the stomata may close early, around noon. The transpiration curves may then have two maxima as shown by Fig. 9.5.

The number of stomata can amount to several hundreds per square millimeter of leaf surface. At normal degrees of opening, only about 1–2% of the surface is open. Nevertheless, transpiration is often very consider-

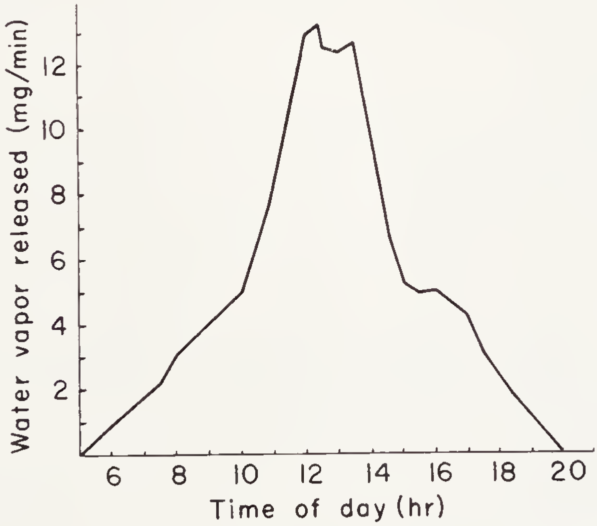

FIG. 9.5. Daily course of transpiration of a mallow leaf. [After Koch, from Huber (1956).]

able compared with evaporation from a free water surface. This is due to the so-called edge effect: Each stoma has a much larger diffusion field (water vapor dome, Fig. 9.4) than a corresponding area of free water surface, and can, therefore, pass more water molecules in unit time. The transpiration/evaporation (T/E) ratio is known as relative transpiration.

The amount of water given off by transpiration by small plants can easily be followed by a transpiration balance. A potometer (Fig. 9.6) is for simultaneous measurement of water uptake; the amount of water taken up is read off the calibrated capillary tube of this instrument. The total transpiration depends on the area as well as on external factors so that no average values for transpiration can be given. A sunflower well supplied with water will transpire about 1 liter of water on a dry warm day.

The main task of the stomata is regulation of the gas exchange for photosynthesis (see p. 214), and transpiration is, therefore, primarily a necessary evil for the plant. However, under conditions of strong insolation the transpiration can exert an important beneficial effect, preventing the leaves from overheating. The transpiration stream or pull (diffusion pressure deficit) also serves the purpose of materials transport within the plant.

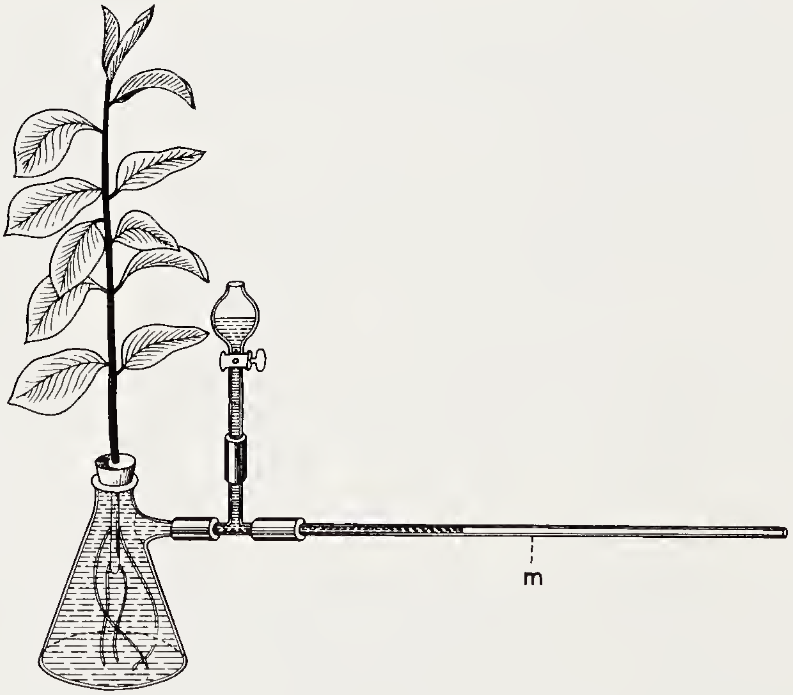

FIG. 9.6. Potometer. m, Measuring capillary tube.

GUTTATION

Apart from the release of water vapor, many plants release liquid water by a process known as *guttation*. Thus, for example, droplets of water can be observed on the tips of blades of grass after a moist and warm night; these are the results of guttation and not dew drops; fungi, too, excrete water in the form of drops (e.g., *Merulius lacrimans*). In a mycelium, all the cells are, in principle, capable of guttation. In higher plants, guttation occurs through special water pores or glands, the *hydathodes*, which excrete water partly passively and partly actively (see p. 93).

Water Conduction

The long-distance transport of water from the root to the sites of water release occurs exclusively in the xylem of the vascular bundles. This can be demonstrated by means of a simple experiment. If the cortex is removed from the lower end of a stem and the remaining woody tissue is immersed in water, the leaves remain turgescent. If, however, the wood is removed and only the cortex is immersed, the leaves will soon wilt. When dye solutions ascend in a stem, only the wood becomes stained. Transport of dyes also allows an estimation of the rate of water conduction. This rate is of the order of 1–10 meters per hour, but in lianas it can amount to over 100 meters per hour. More recently, radioisotopes or thermoelectric methods have been used for the estimation of similar rates of water conduction.

The driving force behind this water movement, which proceeds against gravity over long distances, is the suction due to transpiration. Due to the continuous loss of water, whether by cuticular or by stomatal transpiration, the intercellular spaces and mesophyll cells usually have a water deficit; this deficit is made good either osmotically or by capillary water transport in the cell walls of the ends of vascular bundles (Fig. 9.4). The capillary water columns in the vessels are then moved by suction. This often involves considerable heights (in the giant sequoia, it even exceeds 100 meters), although one would expect that water columns rising in the vessels would break off at heights above 10 meters, which would correspond to atmospheric pressure. This is prevented by the cohesive forces between water molecules, but it is essential that no air should penetrate the vessels. The bundles of the xylem are free from intercellular spaces; this, for example, helps to prevent the entry of air.

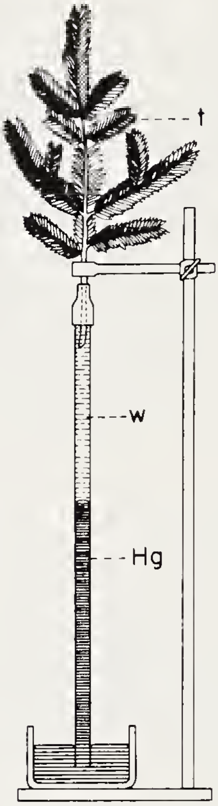

FIG. 9.7. Demonstration of suction due to transpiration. The lower end of a *Taxus* stem is connected to a vertical pipe filled with water. The lower end of the pipe is immersed in a beaker containing mercury. The mercury rises as a result of transpiration. Hg, Mercury; t, *Taxus* stem; w, water. [After Schmeil and Seybold (1945, p. 73).]

The suction resulting from transpiration can be demonstrated by the following experiment: Connect a stem, say that of a yew (*Taxus baccata*) to a vertical pipe filled with water (Fig. 9.7), with the exclusion of air, immerse the lower end of the pipe in a bowl filled with mercury. The mercury will rise in the pipe to over 760 mm as a result of transpiration suction. The mecury will also rise if the *Taxus* stem is replaced by a porous body made of clay or gypsum.

Uptake of Mineral Salts

Minerals salts can also be taken up all over the surface of the plant, and this is utilized in practice in the foliar application of fertilizers. In aquatic plants, however, only the roots are in constant contact with the soil minerals, and the root must be regarded as the primary salt-uptake organ.

Since, generally speaking, salts can only be taken up in the form of ions, they must be dissolved in water. Corresponding to the elemental composition of plants (see pp. 1–2), the following ions are required: the cations K^+, Ca^{2+}, Mg^{2+}, and Fe^{2+} (or Fe^{3+}); and the anions NO_3^-, SO_4^{2-}, and PO_4^{3-}. All these ions are present in the Knop nutrient solution, which consists of 1 g $Ca(NO_3)_2$, 0.25 g $MgSO_4 \cdot 7H_2O$, 0.25 g KH_2PO_4, 0.25 g KNO_3, and traces of $FeSO_4$ in 1 liter of water. Higher plants reared in containers filled with this solution will develop normally, but omission of one of the above ions or its replacement by another (e.g., the replacement of K^+ by Na^+) soon results in severe damage and deficiency symptoms which demonstrate emphatically the importance of the respective ions. When working with highly purified chemicals, it is necessary to add some further elements, such as Mn, Cu, B, and Mo (required in very small quantities). The physiological role of many of these trace elements is still unclear, but their complete absence likewise results in deficiency symptoms. (Grayspot in oats is due to a manganese deficiency, and heart-rot in beets to a boron deficiency.)

It is important that the ions should be offered in balanced proportions, as certain ions by themselves may be toxic even when they are essential to the plants (ion antagonism, see p. 32). The total concentration must not be too high on osmotic grounds. The salt uptake is strongly pH-dependent, and the pH of the nutrient solution must be as near the optimum as possible; however, this value varies somewhat from plant to plant. Thus the optimum soil pH for oats is 5 (i.e., oats are acidophilic) while the optimal pH for barley, which is basophilic, is approximately 8. Potatoes, on the other hand, are within certain limits, insensitive to pH variations and thrive in the entire 5–8 pH region.

The mechanism of ion uptake is complex, and the current ideas on this subject are still largely hypothetical. Basically, ion uptake can occur even against concentration gradients. In the cell sap of the vacuole, the salt concentration is usually higher than in the surrounding medium. The selectivity of ion uptake also speaks against a simple diffusion process. Thus, plants immersed in an ammonium chloride solution, which naturally contains H^+ and OH^- ions besides NH_4^+ and Cl^-, will only take up NH_4^+ and OH^- but not the H^+ and Cl^- ions. The solution will, therefore, eventually become acidic so ammonium chloride is referred to as a physiologically acid salt.

According to the present state of knowledge, ion uptake can be divided into a passive first stage and an active uptake and storage. The former begins with free movement of ions into the "free space," which consists mainly of the cell wall capillaries. This is followed by adsorption of the ions onto the outer boundary layer of the plasma; this stage is also passive, i.e., it does not need an expenditure of energy. It apparently follows the principle of exchange adsorption, i.e., ions of the same sign are exchanged for one another. When this happens, ions with a higher affinity for the surface displace those having a lower affinity.

It is generally assumed that ions are adsorbed on certain "carriers" found in the plasma boundary layers. The chemical nature of these carriers is still unknown, and it is not clear whether they are specific for certain ions or whether various ions can compete for the same carrier. There are many indications that at least the carriers for cations and for anions are not identical.

Even less is known about the successive active stage of ion uptake. It is only certain that it requires an expenditure of energy (so-called salt or ion respiration). The way in which the ion uptake is related to the respiratory cycle can only be conjectured and will not be discussed here.

Materials Transport

IONS

After being taken up by the rhizodermal cells, the ions must be transported to the sites of utilization, especially to the foliage leaves and meristems. The mechanism of transfer from cell to cell through the cortical tissue is unknown, but it probably proceeds in a way similar to the uptake of salts, i.e., by diffusion, mass flow, and an expenditure of energy. The ions are then secreted, again actively, by the parenchymatous cells of the vascular bundles into the neighboring vessels, where they are passively carried along over long distances in the transpiration stream. At the sites of utilization transport (diffusion) from cell to cell again takes place. Ion transport can also occur to some extent in the sieve tubes.

ION EXCRETION

Ion excess can also occur in the tissues, as the selective ability of the roots for ions is not absolute; moreover, the ion requirements of plants alter in the course of their development. The redundant ions can either be precipitated in the form of sparingly soluble salts in the cell sap (Fig. 4.1) or they can be excreted through the outer walls of the epidermis and the cuticle and be leached out by rainwater. In some halophytes there are special salt glands.

ORGANIC MATERIALS

The transport of assimilates (see p. 216) also occurs in the vessels by utilizing the transpiration stream as shown by the example of the exudates (p. 183). The sieve tubes must, however, be regarded as the usual channel for transport which can be upward or downward. The widespread net of sieve elements connects the sites of synthesis with the sites of storage and of utilization. All assimilates can only be transported in solution. The most important transportable forms of carbohydrates are sucrose and, to a lesser extent, raffinose. The fats, too, are apparently transformed into carbohydrates for the purposes of transport (see p. 230). Apart from carbohydrates, a large number of organic compounds have been identified in the sap of sieve elements: amino acids, carboxylic acids, nucleic acids, etc. Transport of growth substances, vitamins, and other active materials also seems to proceed over certain distances in the vascular elements. The velocity of transport is very variable, ranging between a few centimeters and some meters per hours, and it is, therefore, often of the same order as the velocity of the transpiration stream. Views on the transport mechanism are still divergent. Many authors assume that the transport is passive, in the nature of a mass transport, where matter moves in a closed osmotic system from sites of high to ones of low osmotic pressure (concentration). Others, however, think it more likely that the transport is active, as the transport of many substances can be inhibited by blocking respiration; the transport, therefore, seems to require an expenditure of energy. It is possible, however, that the active phase is restricted to secretion of the organic compounds into the sieve elements from the surrounding tissues; the transport in the sieve elements could then be passive. The transport of organic materials from cell to cell, like the transport of ions, must also be regarded as an active process.

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Chapter 10

Energy Procuring and Synthetic Processes in Autotrophic Plants

As has already been explained in Chapter 1, organisms are made up of a great variety of organic compounds. Each of these compounds carries a certain amount of energy which varies from case to case, and this energy is released when the respective molecules are broken down; conversely, energy must be supplied in the process of synthesis. Organisms can be classified as heterotrophic and autotrophic according to whether they acquire the energy required for synthetic reactions exclusively from the decomposition and transformation of organic materials taken up from the environment, or whether they can also utilize other sources of energy. Apart from men and animals, many plants are heterotrophic, e.g., the fungi and the majority of bacteria. Autotrophy, on the other hand, is restricted to plants. In the great majority of cases, the energy requirements of autotrophic plants are met by solar radiation.[1]

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[1] Green plants utilize mainly the visible region (i.e., between 400 and 720 nm) of the electromagnetic spectrum for photosynthesis and reference is therefore usually made to light, which is also reflected in the term "*photo*synthesis." However, nowadays it is known that many physiological processes are also affected by invisible rays (e.g., ultraviolet or infrared). It is therefore preferable to use the more general term, radiation.

Such plants are known as photoautotrophic and the process of energy procuring itself is referred to as *photosynthesis.* However, some lower organisms are able to oxidize inorganic materials and to use the resulting energy for the synthesis of organic substances. These are said to be chemoautotrophic, and the process itself is called *chemosynthesis.*

The importance of the photosynthetic process for our planet can hardly be overestimated if it is remembered that practically all organic compounds on Earth have been and still are synthesized by this process. This meas that in the final analysis all heterotrophic organisms profit by it too. If the photosynthetic process came to a halt, it would mean the end of all life.

All these syntheses, transformations, and decompositions are chemical reactions,[2] and it is therefore impossible to obtain an idea of the course of these reactions and the energy changes involved before discussing the reactions themselves. However, only the most important fundamental principles can be outlined here. For further details the reader is referred to textbooks of biochemistry.

Chemical Reactions and Energy Transfer in Plant Cells

Like all chemical processes, biochemical reactions tend toward a state of equilibrium. For a general reaction of the type

$$\mathrm{A} + \mathrm{B} \rightleftharpoons \mathrm{C} + \mathrm{D}$$

the equilibrium can be characterized by an equilibrium constant, K

$$K = \frac{[\mathrm{C}] \times [\mathrm{D}]}{[\mathrm{A}] \times [\mathrm{B}]}$$

The symbols in brackets represent the concentrations of reactants A and B and products C and D. The equilibrium is shifted to the left or to the right depending on whether K is smaller or greater than unity. It may be displaced completely to one side, e.g., to the side C + D, and the reaction then goes practically to completion. This would mean that after the equilibrium has been reached the reaction mixture contains almost exclusively the reaction products C and D and only very small amounts of A and B.

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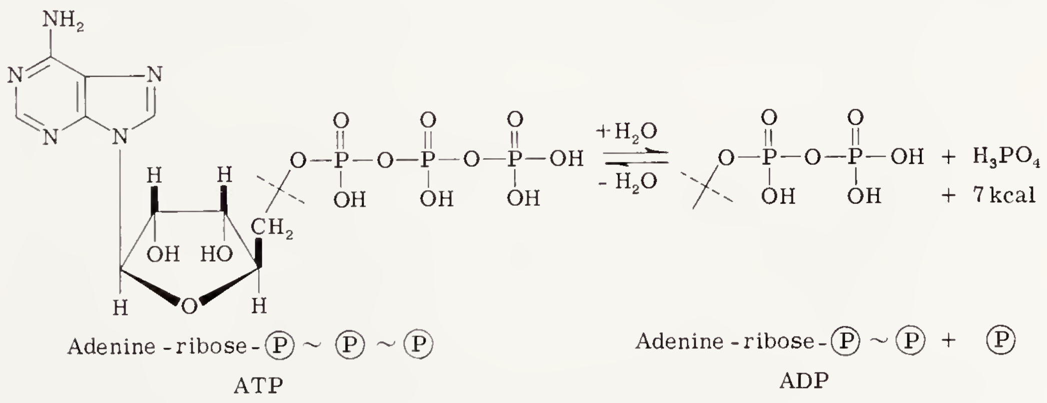
[2] These reactions occur in the living organism and are therefore usually referred to as biochemical reactions.

If, therefore, the reactants A and B are brought together, the reaction will proceed until equilibrium has been reached. This change is accompanied by a change in the energy state, because a reaction can proceed spontaneously only if it is accompanied by a decrease in the potential energy of the reacting substances. Such reactions, therefore, release energy, i.e., they are *exergonic,* as are all spontaneous reactions. This energy, which is reversibly stored in a chemical system and which is released in the course of the reaction, i.e, made available for the establishment of another thermodynamic potential, is known as the *free energy* of the reacting system.

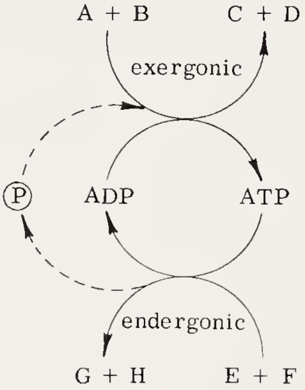
If the reaction is to proceed in the opposite direction, i.e., against the energy gradient, energy in suitable form must be supplied in exactly the same quantity as is released in the exergonic reaction. Such reactions are therefore *endergonic.*

Both exergonic and endergonic processes occur continuously in the cell; this results in a continuous release and/or absorption of energy. Energy-transfer substances are therefore required, which can store reversibly certain amounts of energy in the form of energy-rich compounds. Several such energy-rich compounds have in fact been isolated from organisms. This discussion will be limited to adenosine triphosphate, which is the most common energy carrier.

Adenosine triphosphate, commonly referred to as ATP, is a combination of adenine, a purine-type substance (see p. 13) and a ribose molecule; this is esterified in position C-5 with three phosphoric acid radicals joined to one another with the elimination of water. The two bonds joining the phosphate groups are rich in energy, each of them having an energy of about 7 kcal/mole. This energy is released on *hydrolysis* (chemical addition of water), i.e., on the removal of one phosphate radical, a process resulting in the formation of adenosine diphosphate (ADP) and ortho-

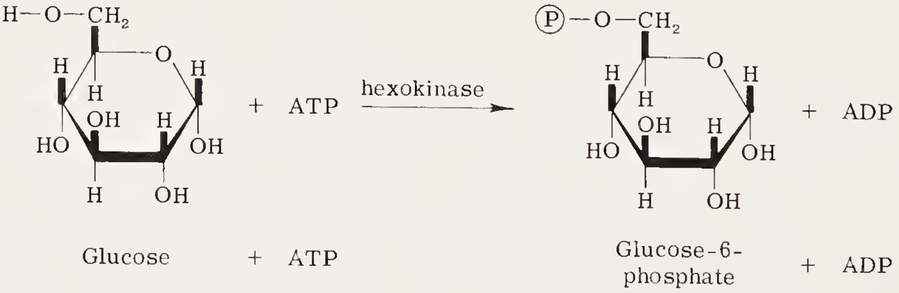


phosphate and—when repeated—of adenosine monophosphate (AMP) and pyrophosphate. ATP can be regenerated with the uptake of energy and the appropriate phosphate radical. The ATP–ADP cycle, which is of primary interest, proceeds therefore according to the scheme shown in the diagram. Guanosine is known to form similar compounds and to undergo similar reactions (GMP, GDP, GTP, see p. 228).



Energy transfer

ATP contains high-energy bonds and can therefore transfer certain groups onto other organic compounds, described generally as substrates. The following example shows the transfer of the orthophosphate group to glucose; glucose-6-phosphate and ADP are formed in the process. The enzyme hexokinase (see below) also takes part in this reaction. Transfer of the phosphate radical activates the respective substrates. The phosphate donor is almost invariably the ATP molecule. Such *phosphorylation processes* play an extremely important part in cell metabolism.



It follows from what has been said above that a closed reaction system can only supply energy and so perform work as long as it is approaching some state of equilibrium. When this state has been reached, the system is as it were in a state of rest. It is obvious therefore that a closed system would soon become useless for maintaining the metabolism of the cell.

In fact, however, equilibrium is not reached in the living cell. Metabolism usually involves a series of reactions coupled in the sense that one reaction utilizes the reaction products of another, which itself draws its components from another reaction, etc. These are therefore open reaction systems in which reactants are continuously supplied from outside and the reaction products are steadily removed. This results in a continuous state of disequilibrium, so that the reaction continues to proceed in the same direction. This condition is described as a steady state. In the final analysis, the sum total of life processes can be regarded as a steady state, to which fresh materials are continuously being added as nutrients; these are then transformed in innumerable coupled chemical reactions.

Biocatalysis

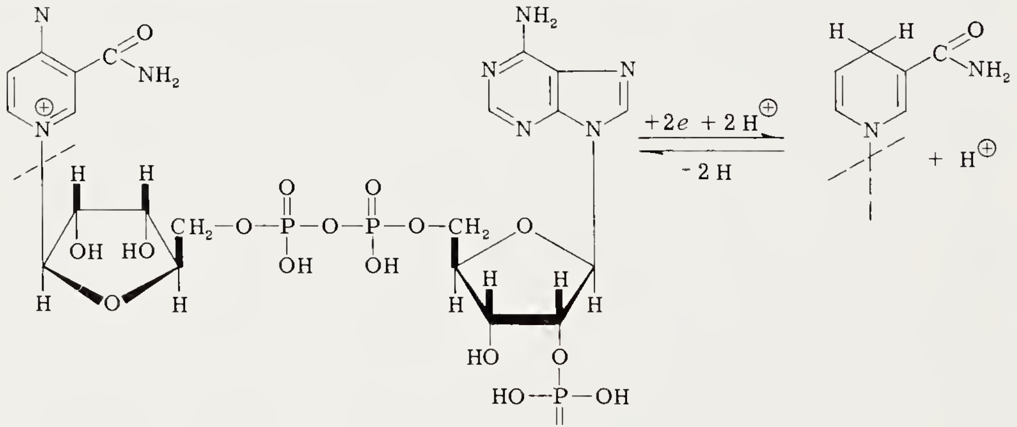
Reactions proceed spontaneously from states of high to those of low energy, and it could therefore be expected that all organic compounds, often quite rich in energy, would continue to react with the available oxygen until the state of lowest energy content has been reached, i.e., until H_2O and CO_2 have been formed as the end products. This, however, is not the case as most carbon compounds are metastable and therefore do not react with oxygen in the biological temperature range. To induce them to react, they must first be activated by the addition of energy; this can occur outside the organism, e.g., by heating. One of the forms of activation that occurs in the organism is phosphorylation, which has already been discussed.

Activation of many organic compounds requires quite large amounts of energy and the cell therefore utilizes a principle now widely used in technology: the principle of *catalysis*. By definition, catalysts are substances which, when present in very small amounts, bring about large transformations without themselves appearing in the end products and without undergoing permanent changes They act as accelerators of reactions by reducing the activation energy necessary for the given process to occur. The reaction products may themselves catalyze the reaction, this situation being known as autocatalysis.

The biochemical catalysts of the cell are the *enzymes*. These are conjugated proteins which consist of a protein component, the apoenzyme, and a prosthetic group. Functionally, they constitute a unit which is also known as the holoenzyme. Enzyme action is specific, i.e., enzymes catalyze only certain particular reactions (reaction specificity) and between particular substrates (substrate specificity).

The prosthetic groups, whose chemical nature varies widely in the various enzymes, are also known as coenzymes. Nowadays the term coenzyme is usually applied to described active groups that can be separated relatively easily from the holoenzyme, while the prosthetic groups are bound strongly to the protein component. Coenzymes undergo changes in the course of the reaction, and an additional reaction is required to return them to their original state in which they are capable of affecting the given process; they do not, therefore, correspond exactly to the definition of catalysts given above, but function rather as cosubstrates.

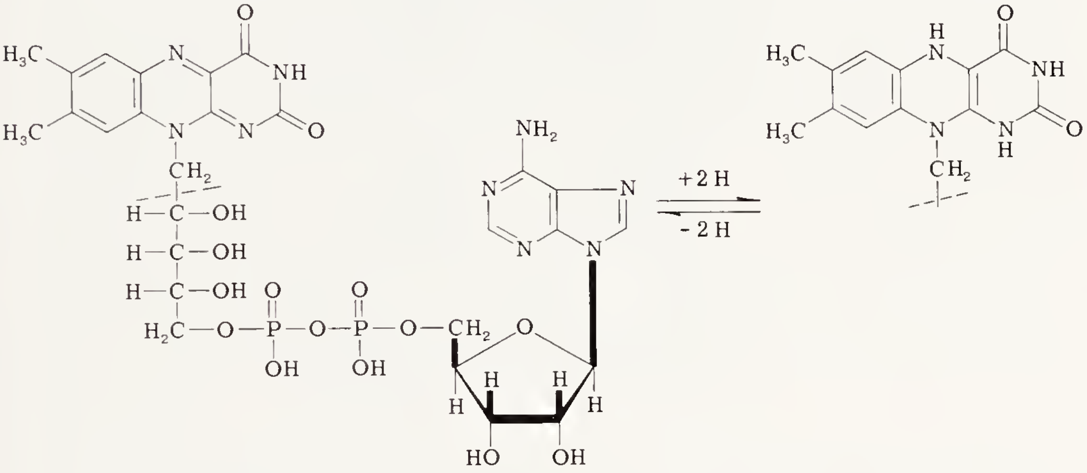
Apart from ATP, whose action has already been mentioned, nicotinamide adenine dinucleotides (NAD for short, previously also known as diphosphopyridine nucleotide, DPN, or codehydrase I) and nicotinamide adenine dinucleotide phosphate (NADP for short, previously also known as triphosphopyridine nucleotide, TPN, or codehydrase II) serve best as examples of the mode of action of coenzymes. As shown by the formula below, the NAD molecule consists of nicotinamide, adenine, and two ribose molecules joined to each other by a bridge consisting of two phosphoric acid molecules. In NADP there is also a third phosphoric acid radical on the ribose molecule of the adenosine. Both carry a positive charge in the pyridine ring of the nicotinamide, and they are therefore designated more correctly as NAD$^+$ and NADP$^+$, respectively.



NADP⊕ NADPH + H⊕

As can be seen from the formula, the nicotinamide adenine dinucleotides are able to take up hydrogen reversibly, thereby being reduced to NADH + H$^+$ and NADPH + H$^+$, respectively. These therefore act as coenzymes of the dehydrogenases, i.e., enzymes that remove hydrogen from their substrates. The hydrogen is taken up by the coenzymes and is transferred to another substrate in a second reaction, and the coenzymes are reconverted to their oxidized form in which they can once more abstract hydrogen. It must be mentioned in this context that many coenzymes can take part in various reactions, i.e., their reaction specificity is not as pronounced as that of the holoenzymes.

Other compounds active in hydrogen transfer are the flavine nucleotides; these include flavine mononucleotide (FMN), the active group of the "yellow enzyme" (see p. 230), and flavine adenine dinucleotide (FAD). As shown by the diagram, FAD takes up two hydrogen atoms in the isoalloxazine ring of the riboflavine) (see p. 324) is reduced to $FADH_2$.



Oxidized

Reduced

Flavine adenine dinucleotide (FAD)

There are a great number of enzymes corresponding to the variety of biochemical reactions which constitute the metabolism of the cell. Many of them have already been purified. For ribonuclease, the enzyme that catalyzes the depolymerization of RNA, even the amino acid sequence is known (see p. 17). Originally enzymes were named after the substrates in the transformation of which they took part, by the addition of the ending "ase" to the name of the substrate. For example, the enzyme splitting maltose into two glucose molecules is known as maltase, the enzymes decomposing starch are known as amylases, and so on. Nowadays enzymes are grouped according to their functions and are named accordingly. The hydrolases catalyze hydrolytic cleavage of molecules (amylase, maltase, etc.), transferases transfer groups of molecules (e.g., hexokinase, see p. 198), oxidoreductases take part in redox processes, etc.

The mode of the action of an enzyme is modeled mechanically in Fig. 10.1. A hydrolase has been chosen as an example; this enzyme splits molecules into two halves with the uptake of water. During this process the molecule is adsorbed on the surface of the enzyme. The surface

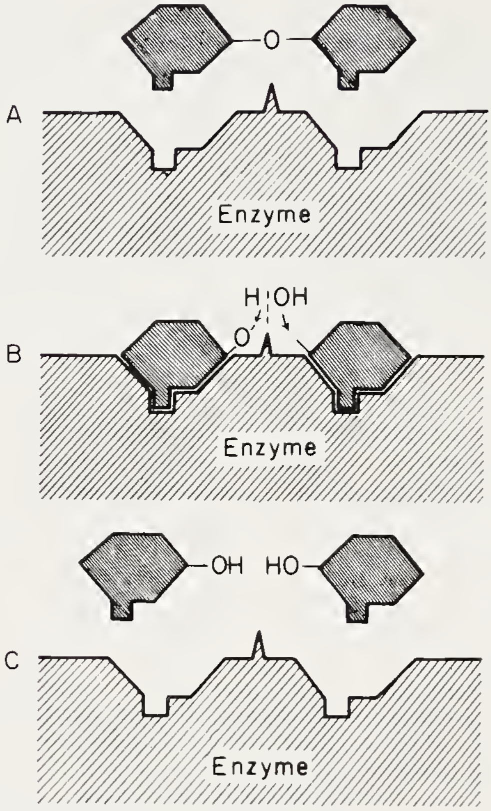


FIG. 10.1. Schematic action of an enzyme. (A) The original uncleaved molecule approaches the surface of the enzyme. (B) Molecule adsorbed on the surface of the enyme and hydrolyzed (cleaved) . (C) The resulting half molecules desorb from the enzyme surface. The diagrams of the molecules are only symbolic and do not represent any specific compound. The "lock and key principle" is a three-dimensional concept and so a two-dimensional figure is only an incomplete representation of the true state of affairs.

structure of the enzyme is such that only molecules having a certain specific steric configuration can be "fitted," like a key in a lock (substrate specificity). If the configuration of another molecule is similar, this "pseudo" substrate can also be transformed. Often, however, the "pseudo" substrate is merely adsorbed on the enzyme surface but is not transformed. This results in blocking of the particular enzyme, as its surface remains occupied (competitive inhibition).

Photosynthesis

Lebedev (1921) pointed out that since the discovery of chemosynthesis in bacteria showed that CO_2 fixation could occur in the dark, it was an error to consider CO_2 assimilation as peculiar to photosynthetic cells. Only 40 years after the discovery of the Wood-Werkman reaction and the use of tracer isotopes in the past 20 years was it finally recognized that CO_2 assimilation is a very general cell process. "*All living cells, photosynthetic and non-photosynthetic, autotrophic and heterotrophic, assimilate CO_2 but differ as to the source of energy that must be expended during this process* (Arnon, 1961)."

In photosynthesis, radiant energy is absorbed and transformed into chemical energy. Chemically, the light process consists of two steps: (1) the photooxidation of water where hydrogen is split off from the water molecule and oxygen is released. The reaction supplies electrons for noncyclic phosphorylation where (2) TPN is reduced and ATP is formed. In the *dark* reaction hydrogen is transferred to carbon dioxide and is bound in a metastable carbon compound. Carbon dioxide therefore acts as a hydrogen acceptor. The often used expression "assimilation of carbon dioxide" does not, therefore, quite represent the true state of affairs. The separation of hydrogen from oxygen is an endergonic reaction which requires the supply of exactly the same amount of energy as is released during formation of water from hydrogen and oxygen. The material and energy balance of photosynthesis is therefore given by the equation (see also p. 212).

$$6CO_2 + 12H_2O \xrightarrow{675\ \text{kcal}} C_6H_{12}O_6 + 6O_2 + 6H_2O$$

Compared with the amount of water available, the amount used in photosynthesis is small; it is therefore difficult to show that it is involved in the photosynthesis reaction. The participation of the other reactants in the overall equation can, on the other hand, be verified by simple basic experiments.

NECESSITY OF CO_2

Plants reared in a CO_2-free atmosphere, e.g., under a belljar in the presence of sodium hydroxide, soon stop developing and die in spite of an adequate supply of light. The CO_2 utilized by plants in the presence of light can be measured directly, e.g., by chemical, manometric, or electrochemical methods, by estimating the absorption of $^{14}CO_2$, or by an infrared absorption spectrometer.

SYNTHESIS OF CARBOHYDRATES

The sugar synthesized in the first place is transformed there and then into starch, so that the carbohydrate synthesis can be detected by the

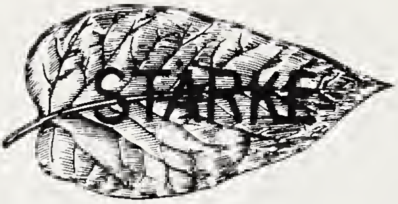


Fig. 10.2. Identification of starch produced in the leaf (Stärke = starch). The leaf was covered during the period of illumination by a sheet of opaque material with the word "Stärke" cut out. Starch has been synthesized only at these illuminated sites, as demonstrated by the iodine–starch reaction. (After Sierp.)

iodine–starch reaction. This can be done by covering a leaf that had been kept in the dark for some time with a sheet of opaque material with some figures or letters cut out to form a stencil. The leaf is then exposed to light. After some time the production of starch can be demonstrated by killing the leaf tissue by immersion in boiling water and treating it with a solution of iodine in potassium iodide. The letters then appear blue-black on a background bleached by immersion in hot alcohol (Fig. 10.2).

Formation of Oxygen

The gas bubbles released by an illuminated aquatic plant, e.g., the water weed *Elodea canadensis*, can be collected in a test tube (Fig. 10.3); oxygen can be identified by the pine splinter ignition test. The oxygen can also be estimated by the more accurate methods mentioned already in connection with CO_2. By means of these methods, the molar ratio of CO_2 utilized to the O_2 released can also be measured; the value of the assimilation quotient O_2/CO_2 then turns out to be 1, as required by the overall equation. The need for the radiation can very easily be demonstrated: None of the processes referred to above will proceed in the dark.

Photosynthesis utilizes only a fraction of the energy arriving per unit area and in unit time at the Earth's surface. The photosynthetic productivity of 1 meter^2 of leaf surface is of the order of 1 g of carbohydrate per hour.

Historical Note

As early as 1727, the English parson Stephen Hales expressed the opinion that plants derive their nutrients from the air. The first photosynthetic experiments were carried out by Priestley in 1771–1772. Priestley showed that animals and plants thrive well enough when enclosed together in an airtight space, while animals alone die off after a short time.

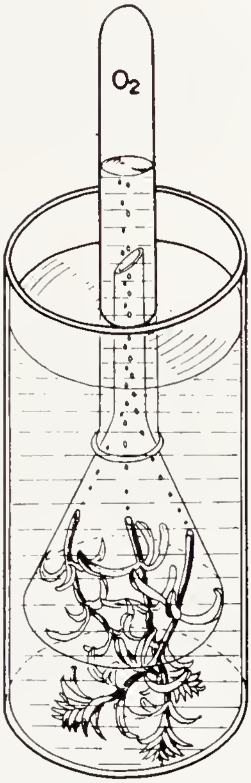


FIG. 10.3. Collection of oxygen released by an illuminated shoot of water weed (*Elodea canadensis*) in a test tube.

He therefore concluded that plants "regenerate" the air "spoiled" by animal respiration. Ingenhouz, in 1779, recognized the light dependence of this process, and also that it was restricted to the green parts of plants. In 1782, Senebier established the special activity of red radiation and attempted the isolation of chlorophyll for the first time. Finally, De Saussure distinguished respiration and assimilation and was the first to measure the assimilation coefficient by gravimetric techniques. The structure of chlorophyll was partly established by Willstätter and Stoll, and also by Hans Fischer who presented the complete chlorophyll formula in 1939. Chlorophyll has also since been synthesized *in vitro*. The intensive research of recent years and decades has now led to a deeper understanding of the photosynthetic process.

Inspection of the overall equation would seem to suggest that photosynthesis is a relatively simple process, but exact analysis has shown that many individual reactions are involved which interact in a complicated manner. Only some of them are photochemical in the strict sense of the term, while others proceed also in the dark. The usual distinction between photochemical and other reactions is, however, only partially justified, since here the photochemical stages are essential prerequisites of those that can also proceed in the dark. The broad outlines of the process are today more or less understood, but the details of many individual steps are still not quite clear.

ABSORPTION OF RADIATION

The photosynthetically active radiation is absorbed by the chromatophore pigments, primarily chlorophyll. This can be demonstrated very elegantly by Engelmann's bacterium experiment. The spectrum of visible light produced by a prism is projected onto an algal thread (*Chladophora, Oedogonium,* or other). The bacteria in the preparation are then attracted aerotactically (see p. 396) by the photosynthetically produced oxygen to a degree depending on the photosynthetic activity of the corresponding spectral region. The most active region can be compared with the absorption curve of chlorophyll obtained by the use of a spectrophotometer (Fig. 10.4), and it is then found to coincide with the absorption maximum of chlorophyll in the red region of the spectrum. On the other hand, blue radiation, which is also strongly absorbed by chlorophyll, has a relatively small effect. In other cases, blue light is rather more effective.

It can be seen from Fig. 10.4 that the absorption curves of chlorophyll a and b differ mainly in that the two maxima in the red and blue regions are nearer to each other in chlorophyll b. The intermediate green spectral region is hardly utilized by either of the chlorophylls, and in the infrared region there is no absorption at all. A thin layer of chlorophyll solution in transmitted light therefore appears green, while a thick layer appears red; in the latter case, even the green radiation is largely absorbed. Several superimposed leaves also appear red in transmitted light.

The most important pigment in photosynthesis is chlorophyll a. It occurs in all photoautrophic organisms except purple bacteria. Chlorophyll b, however, is lacking completely in many algal groups, and therefore cannot be regarded as essential. It is interesting that other photosynthetic pigments occur in these organisms, e.g., chlorophyll c and d, and the biliproteins which have already been mentioned (see p. 48). All these pigments, including chlorophyll b, are known as accessory pigments. It is now generally assumed that in photosynthesis two photochemical reactions are coupled together; the various pigments take part in these reactions to various extents (see below).

The function of carotenoids in photosynthesis is still unclear. As shown by the absorption spectrum of β-carotene (Fig. 17.15), they absorb only

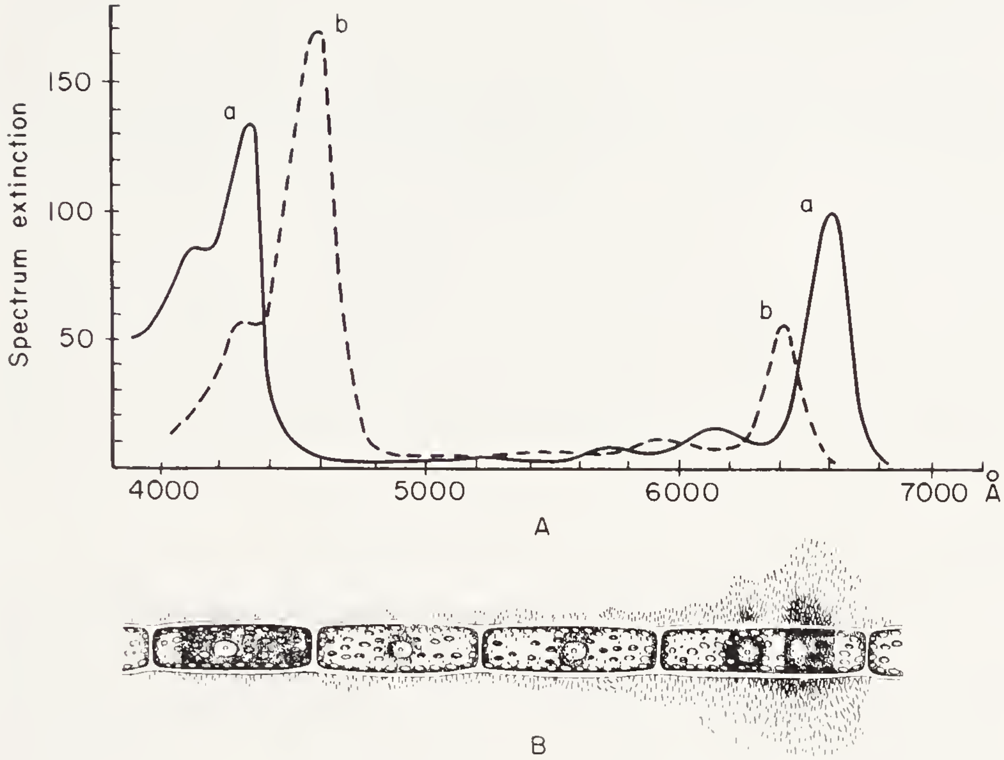


Fig. 10.4. (A) Absorption spectra of chlorophyll a and b in ether. (B) Engelmann's bacterium experiment. A spectrum is projected onto a thread of green algae (*Oedogonium*). Strong accumulation of aerophilic bacteria can be observed only in the red region. The main absorption regions of the chlorophyll, shown darkened in the diagram, do not exactly coincide in wavelength in the living cell and in solution. (After Zscheile and Pfeffer.)

in the short-wavelength region, i.e., in the violet and blue regions. Some carotenoids, such as fucoxanthine which occurs in diatoms and in brown algae, can transfer their absorbed radiant energy to chlorophyll a; they therefore take part indirectly in the photosynthetic process. Others, however, appear to have protective groups preventing the photooxidation of chlorophyll.

On absorbing a quantum of light, chlorophyll a is raised to an excited state, which is described as the first or second singlet state depending on whether red or blue radiation has been absorbed. The second of these states has a higher energy than the first, corresponding to the greater energy content of blue light quanta (see p. 5). The absorbed energy can be released again in the form of photons as fluorescent light, it can be dissipated as heat, or it can be transformed into chemical energy.

PHOTOPHOSPHORYLATION

Isolated chloroplasts were found to synthesize ATP without the aid of mitochondria (Arnon, Allen, and Whatley, 1954). Is light-induced ATP formation in chloroplasts comparable to oxidative phosphorylation by mitochondria as discussed in Chapter 3? Two fundamental differences are apparent: (1) ATP formation in chloroplasts occurs without using oxygen; and (2) without chemical substrate to supply energy for forming pyrophosphate bonds of ATP. The term *photosynthetic phosphorylation* was given to light-induced ATP formation in chloroplasts to distinguish it from oxidative (respiratory) phosphorylation by mitochondria as well as anaerobic phosphorylation in substrates that occurs in glycolysis (Arnon, 1955).

Cyclic Photophosphorylation and ElectronTransport

In the course of biochemical evolution, photosynthesis first emerged as a process for converting light energy into ATP, and the "primitive photosynthesis" only much later became a process linked to CO_2 reduction (Arnon, 1961). *Chromatium* cells containing *hydrogenase* localized in the chromatophores and in the presence of molecular hydrogen do not require light for the reduction of pyridine nucleotides, especially DPN. Photosynthesis in *Chromatium* may be summarized as follows:

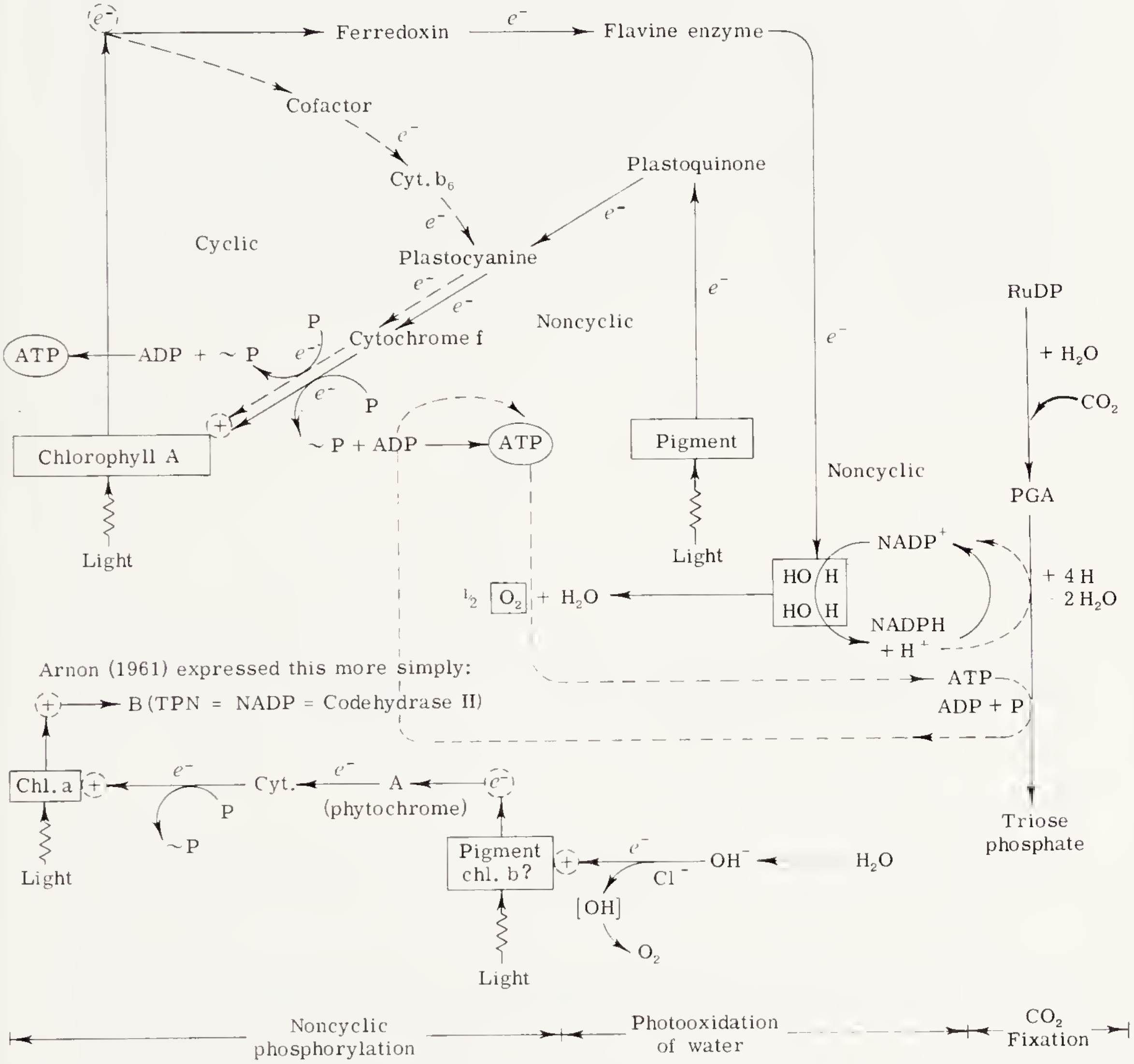
Light phase
Cyclic photophosphorylation
$$n\cdot\text{ADP} + n\cdot\text{P} \dashrightarrow n\cdot\text{ATP}$$
Dark phase
DPN reduction $$2\ \text{DPN} + 2\text{H}_2 \dashrightarrow 2\ \text{DPNH}_2$$
CO_2 assimilation $$\text{CO}_2 + 2\ \text{DPNH}_2 + n\cdot\text{ATP} \dashrightarrow (\text{CH}_2\text{O}) + \text{H}_2\text{O} + 2\text{DPN} + n\cdot\text{ADP} + n\cdot\text{P}$$

Green plants do not ordinarily contain hydrogenase, hence they cannot use hydrogen gas during photosynthesis, as *Chromatium,* for reducing pyridine nucleotide in the dark. Rather they use water (OH^-) as the electron donor.

Noncylic Photophosphorylation and Electron Transport or Photoreduction

Noncyclic photophosphorylation (electrons activated by light do not travel a cyclic path) in higher green plants combines two component photochemical reactions: (1) the auxiliary reaction of photooxidation of water; and (2) the bacterial type of noncyclic photophosphorylation used for photoreduction of pyridine nucleotide and a coupled phosphorylation.

According to our present state of knowledge photophosphorylation consists of two successive, coupled photochemical reactions. The pigment of the first reaction is chlorophyll a, while the second reaction involves (apart from chlorophyll a) the secondary pigments (certainly including chlorophyll b), designated as "pigments" in the following schematic diagram.

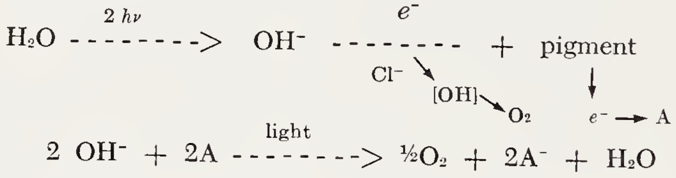


Cyclic and noncyclic phosphorylation and electron transport

The radiant energy absorbed by chlorophyll a is transferred in the form of energy-rich electrons to a redox system, probably ferredoxin, which is thereby reduced. The electrons are then transferred through a flavine enzyme to NADP+ which is transformed with the uptake of two protons into the reduced state NADP + H^+. The second pigment system oxidizes water photochemically, i.e., two light quanta are taken up, and electrons are transferred to a redox substance presumably plastoquinone. Water is thereby decomposed and oxygen is released. The electrons are then transferred from plastoquinone to chlorophyll a in a series of redox systems (plastocyanine, cytochrome f). The electron deficiency of chlorophyll a is then made good so that it can again be excited. The process by which electrons from the photooxidation of water are transferred to $NADP^+$ by the two photochemical reactions and the redox systems of the electron transport chain is known as *noncyclic electron transport.*

It must be pointed out that, although the path of the electrons described above has been well confirmed experimentally, it is still hypothetical to some extent. In particular, the nature of the individual members of the electron chain has by no means been fully clarified. It must therefore be expected that the scheme outlined above will undergo various modifications in the future.

Photooxidation of Water



This reaction supplies electrons at an elevated reducing potential for a second photochemical reaction: noncyclic phosphorylation during which triphosphopyridine nucleotide is photoreduced, coupled with the formation of ATP.

Noncyclic Phosphorylation

$$2A^- + 2TPN + 2H^+ + ADP + H_3PO_4 \xrightarrow[\text{(phytochrome)}]{} TPNH_2 + ATP + 2A$$

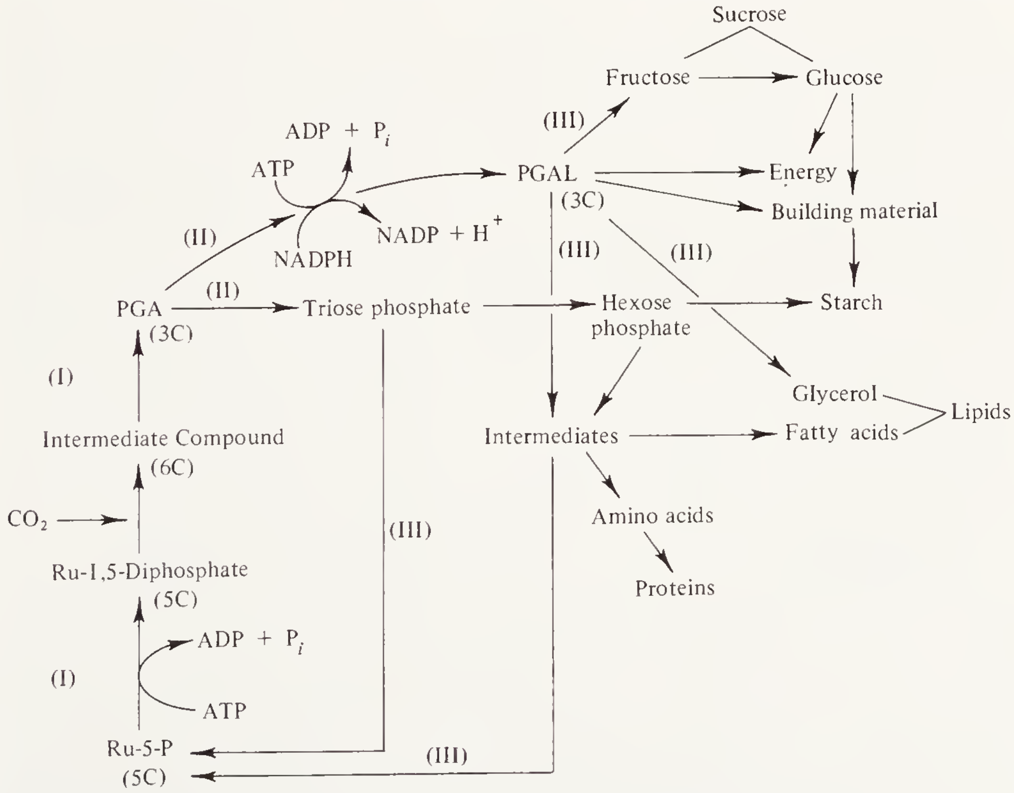
The evolution of one mole of oxygen is accompanied by the reduction of two moles of TPN and the esterification of two moles of orthophosphate.

The *electron transport* between the two photochemical reactions proceeds downhill, i.e., from a higher to a lower energy level. The energy released is taken up partly in the form of ATP and partly as NADPH + H^+. The exact stage in the electron transport chain at which ATP is formed is still unknown, but it is probably at the transfer of electrons from plastoquinone to plastocyanine or to cytochrome f.

Summarizing, it may be said that so-called reduction equivalents, i.e., NADPH + H^+ and ATP, are produced by photochemical reactions and the electron transport chain; they are available for the "reduction of CO_2."

INCORPORATION OF CARBON DIOXIDE

It had been assumed for a long time that six molecules of carbon dioxide combined by reduction and subsequent polymerization to form a glucose molecule. However, Calvin[3] *et al.* showed some years ago that the incorporation of carbon dioxide occurs in a very different manner. The carbon dioxide molecule is first incorporated into a C_5 sugar: ribulose-1,5-diphosphate. This gives rise to a C_6 compound (see diagram) which is unstable and whose exact constitution is therefore unknown. On interaction with carboxydismutase, this compound splits at once into two C_3 molecules of phosphoglyceric acid (PGA), which are then reduced by the available reduction equivalents with the aid of ATP and split out water: This gives rise to triose-3-phosphate, $NADP^+$, and ADP, or to phosphoglyceraldehyde (PGAL). Two molecules of triose phosphate



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[3] M. Calvin received the 1961 Nobel prize in chemistry for this work.

are converted into a C_6 molecule, i.e., a hexose, while the ribulose-1,5-diphosphate is regenerated from further C_3 molecules in a complicated cycle that is the reverse of the glycolysis and Krebs cycles, or (Chapter 11) by the direct oxidation of glucose to ribulose-5-phosphate. Other C_3 molecules, as PGAL, may be converted into glucose or through intermediates some may form ribulose phosphate to renew the cycle.

The process of CO_2 assimilation by isolated chloroplasts follows the same pathway as in algal cells and leaves. *All the reactions of the cycle occur in the dark.*

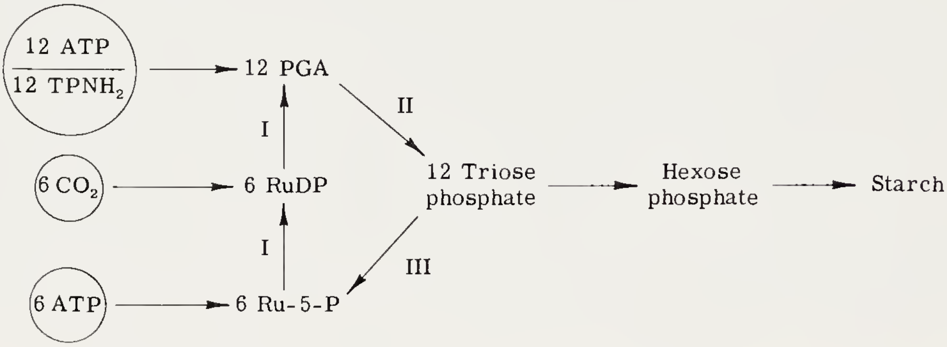
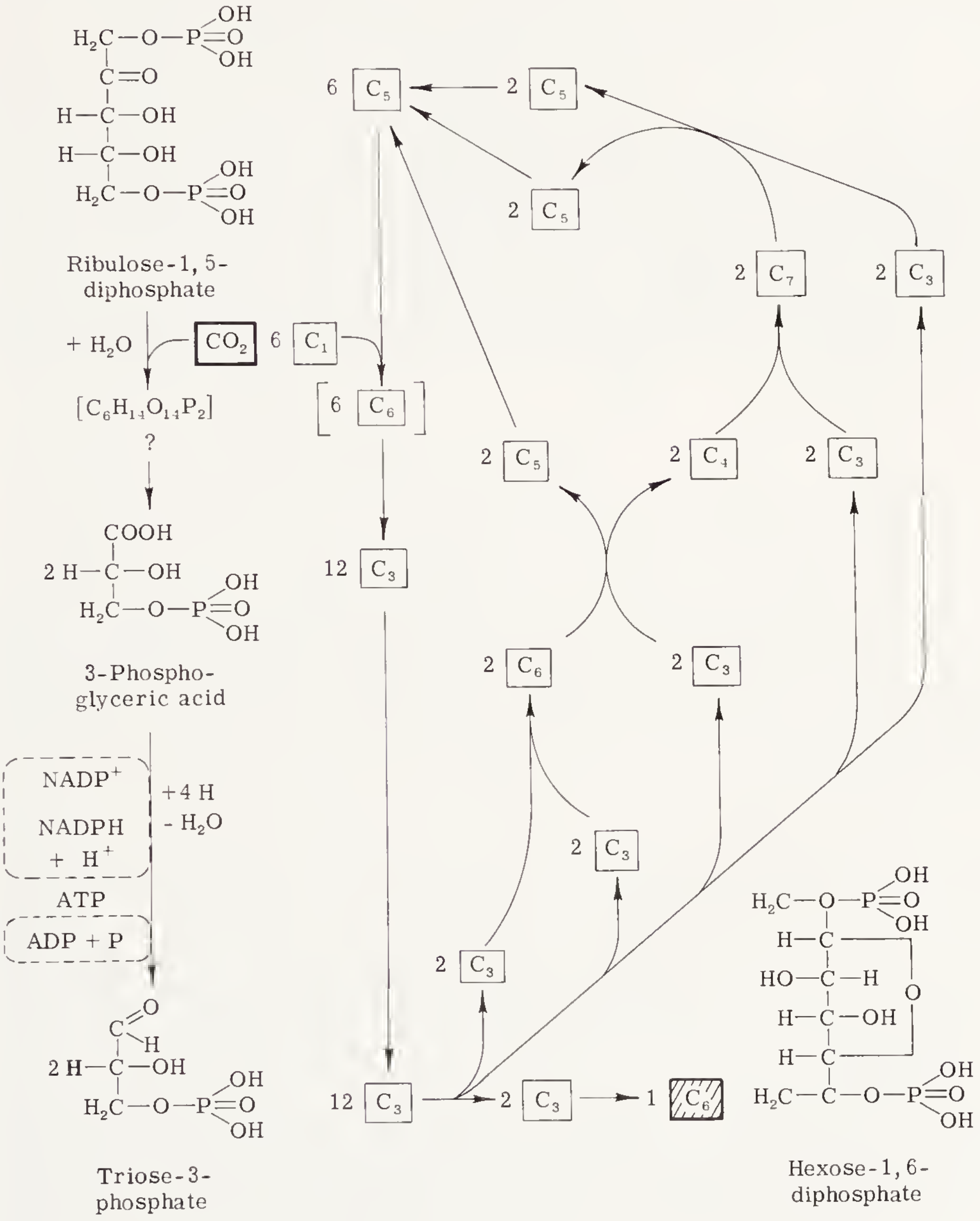


Diagram modified from Arnon (1961) of the reductive carbohydrate cycle in isolated chloroplasts. Not all of the steps may be correct. The cycle consists of three phases: In the *carboxylative phase* (I), ribulose-1,5-phosphate is *phosphorylated* to ribulose diphosphate which then accepts a molecule of CO_2 and splits into two molecules of phosphoglyceric acid; in the *reductive phase* (II), phosphoglyceric acid (PGA) is reduced to triose phosphate and phosphoglyceraldehyde (PGAL); and in the *regenerative phase* (III), triose phosphate is partly converted into Ru-5-P and partly into hexose phosphate and starch, and PGAL may form glucose or through intermediates some may form ribulose phosphate to renew the cycle. The reactions of phases I and II are driven by ATP and $NADPH_2$ formed in the light.

One complete turn of the cycle results in the assimilation of 1 mole of CO_2 at the expense of 3 moles of ATP and 2 moles of $TPNH_2$.

To illustrate the formation of a C_6 compound from 6 CO_2 molecules, 6 molecules of ribulose-1,5-diphosphate are shown in the schematic flow diagram below, which yield 12 C_3 molecules with 6 molecules of CO_2. These will give rise to a C_6 compound (hatched in the diagram), while the remaining 10 C_3 molecules are reconverted into six C_5 molecules. A total of 12 NADPH + H^+ molecules are required for the reduction of 6 CO_2 molecules. Apart from these, ATP is also consumed. The exact quantum requirements of photosynthesis are still uncertain; the values quoted in the literature lie in the range of 4–8 quanta per molecule of oxygen formed.



CO_2 Fixation

PHOTOSYNTHESIS IN PURPLE BACTERIA

It has already been mentioned in the discussion of bacterial cells that there are also photoautotrophic species having chromatophores among the bacteria. The role of chlorophyll a is here taken over by bacterio-

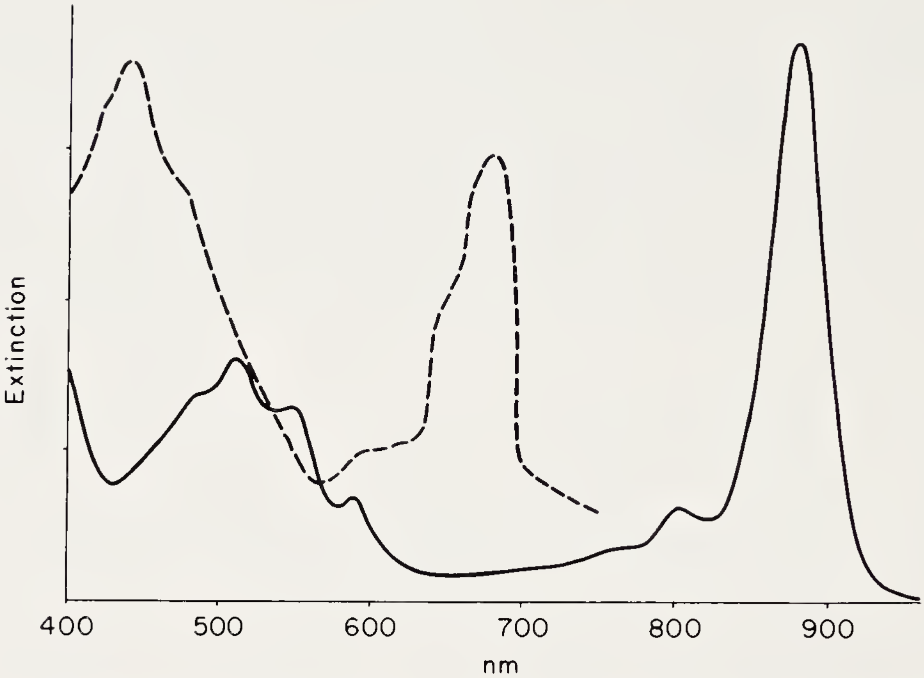


FIG. 10.5. Absorption spectrum of the chromatophores of *Rhodospirillum rubrum*. The maximum in the region between 800 and 900 nm is due to bacteriochlorophyll, while in the short-wavelength region carotenoids are also active. The absorption spectrum of the green alga *Chlorella* is given for comparison (broken line). (After Drews and Allen.)

chlorophyll which differs from chlorophyll a both chemically (see p. 47) and with respect to absorption of radiation. As shown by the absorption spectrum (Fig. 10.5), the main absorption region in the living cell lies between 800 and 900 nm, i.e., in the infrared region (see the remark on p. 193) which cannot be utilized photosynthetically by other photoautotrophic plants.

The photosynthesis in purple bacteria also deserves attention for other reasons. The hydrogen and electron donors in this case are inorganic sulfur compounds, e.g., H_2S (Thiorhodaceae) or organic substances (Athiorhodaceae), so that no oxygen is released. The overall formula for the photosynthesis in the Thiorhodaceae is therefore

$$6\ CO_2 + 12\ H_2S \xrightarrow{\text{radiation}} C_6H_{12}O_6 + 12S + 6H_2O$$

Here the electron donor is the sulfide ion, which is transformed into elemental sulfur according to the equation $S^{2-} \rightarrow S + 2e^-$. This sulfur is then deposited in the cells in the form of the well-known polysulfide droplets (see p. 105). The photosynthesis can therefore be represented by the overall formula

$$6\ CO_2 + 12\ H_2A \xrightarrow{\text{radiation}} C_6H_{12}O_6 + 12A + 6H_2O$$

where A represents any type of hydrogen donor.

The fact that the oxygen released in the photosynthesis of green plants originates from the water and not from the CO_2 (see above) was deduced from the very observation that in the photosynthesis of the Thiorhodoceae elemental sulfur is formed rather than oxygen. This also explains why the equation is written with $12H_2O$ on the left and $6H_2O$ on the right (see p. 201). The above examples show that the oxygen of these 6 water molecules originates from the CO_2.

PHOTOSYNTHESIS IN THE NATURAL HABITAT

The discoveries concerning the photosynthetic process described above were made mainly through experimental studies in the laboratory, which do not normally correspond to natural conditions. In the laboratory all external factors are kept constant as far as possible with the exception of the variable being studied. In nature, on the other hand, photosynthesis proceeds under the influence of local and constantly varying external conditions, which have an appreciable bearing on the photosynthetic process. The most important of these external conditions will now be outlined.

Light

It is obvious that the yield of a photochemical process depends first of all on the prevalent radiation conditions. It can be said quite generally that the rate of photosynthesis increases with increasing radiation intensity. As shown by Fig. 10.6, this continues until the saturation point is reached. The curve then tails off and becomes nearly parallel to the abscissa, i.e., any further increase in the light intensity no longer increases the rate of photosynthesis. The saturation levels differ for the various plant species; they are higher for plants adapted to high intensities (i.e., plants whose leave contain few chloroplasts) than plants that prefer shade. The photosynthesis curve intersects the abscissa at a positive value of light intensity. This intersection point is known as the compensation point, at which the loss of carbohydrates due to respiration is exactly balanced by their production from photosynthesis (see p. 223). The compensation point is lower for shade-living plants than for ones adapted to intense

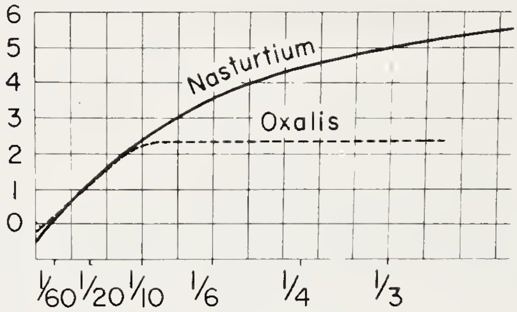


FIG. 10.6. Photosynthesis curve of a plant adapted to intense radiation (*Nasturtium*) and a shade living plant (*Oxalis*) as a function of the incident radiation intensity. Abscissa, fraction of full sunlight; ordinate, intensity of CO_2 assimilation; compensation point, intersection of the curves with the horizontal zero line. (After Lundegardh.)

radiation. The former can therefore survive under radiation conditions under which the carbohydrate balance of the latter is already negative. The light conditions therefore have a decisive effect on both the distribution of plants over the various climatic zones and the colonization of individual locations.

Carbon Dioxide

Since carbon dioxide acts as a hydrogen acceptor and is incorporated into the products of photosynthesis, the rate of the whole process must also depend on the amount of available CO_2. Under natural conditions this should normally be the limiting[4] factor as its concentration of 0.03% in the atmosphere is less than optimal for photosynthesis. In fact, the rate of photosynthesis can in many cases be increased by artificially increasing the CO_2 partial pressure, while leaving the intensity of incident radiation constant. This is made use of in industrial horticultural practice.

Atmospheric Humidity

The entry of carbon dioxide into plants proceeds mostly through the stomata, and the degree of opening of these depends, among other things, on atmospheric humidity (see p. 163). Humidity can therefore also affect indirectly the rate of photosynthesis.

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[4] According to the so-called rule of limiting factors, the efficiency of photosynthesis is determined by the factor present in the minimum quantity, i.e., the factor furthest removed from the optimum. This naturally also holds for other physiological processes (see p. 239).

Temperature

The temperature dependence of photosynthesis follows necessarily from the fact that some of the stages, the dark reactions, are chemical processes having Q_{10} values[5] of 2 or more, while the photochemical reactions with Q_{10} little greater than unity are practically temperature-independent. In fact, the temperature must exceed a certain minimum value before photosynthesis becomes possible at all. The rate of photosynthesis then increases with rising temperature, to reach an optimum past which the rate is reduced when the temperature is raised further; finally the maximum temperature is reached, at which no photosynthesis occurs at all. The shape of the rate–temperature plot is therefore that of a typical optimum curve (see p. 356). The temperature optima of plants in our latitudes lie in the region of 20°–30°C, the minima being near freezing point. It has been found, however, that plants adapted to extreme climates (e.g., lichens) are able to continue photosynthesis at temperatures well below the freezing point. The maxima are in the region of 35°–50°C. The latter are obviously highest in plants adapted to very hot environments.

Chemosynthesis

The essential process in photosynthesis is the exergonic separation of hydrogen from oxygen and hydrogen fixation in the form of a metastable carbon compound, and it should be possible for this process to occur with sources of energy other than light. This is indeed the case in chemoautotrophic bacteria, which obtain their energy from the oxidation of various inorganic substrates; this energy is then used for the synthesis of organic substances. As can be seen from the example of sulfur and iron bacteria, the term oxidation covers not only combination with oxygen but also loss of hydrogen, or, quite generally, removal of electrons. The electron notation can therefore equally well be used to describe the various types of chemosyntheses which are summarized in the following table.

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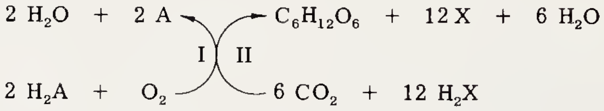
[5] The Q_{10} value is a measure of the temperature sensitivity of a process and is defined as the increase of the reaction rate brought about by a 10°C rise in temperature. The Q_{10} value for temperature-independent processes is 1, i.e., the increase of temperature has no effect on the reaction rate. The Q_{10} values of temperature-dependent chemical processes are 2 or more, i.e., the rate is at least doubled by a temperature rise of 10°C.

Group	Genus	Reaction
Sulfur-oxidizing bacteria	*Beggiatoa*	$2H_2S + O_2 \rightarrow 2H_2O + 2S + 118$ kcal $2S + 2H_2O + 3O_2 \rightarrow 2H_2SO_4 + 286$ kcal
Nitrifying bacteria	*Nitrosomonas* *Nitrobacter*	$2NH_3 + 3O_2 \rightarrow 2HNO_2 + 2H_2O + 158$ kcal $2HNO_2 + O_2 \rightarrow 2HNO_3 + 36$ kcal
Iron-oxidizing bacteria	*Ferrobacillus*	$Fe^{2+} \rightarrow Fe^{3+} + e + 16$ kcal
Hydrogen-oxidizing bacteria	*Hydrogenomonas*	$2H_2 + O_2 \rightarrow 2H_2O + 114$ kcal

The amounts of energy obtained on oxidation vary widely, and varying amounts of substrates (designated as H_2A in the schematic diagram below) must therefore be transformed for the synthesis of equal quantities of organic materials. As the scheme shows, whatever substrate is being oxidized the energy-supplying process is always coupled with the synthetic process in which organic materials are produced from CO_2 and hydrogen; the latter can be obtained from any hydrogen donor H_2X.



Schematic diagram of chemosynthesis

I. Energy-supplying process
II. Synthetic process

Utilization of the Assimilation Products

As has been seen, the first end products of photosynthesis are hexose sugars. Neither utilization on the spot, nor transport to other regions of the plant can keep up with the production of sugar when the photosynthetic process is fully active, so that the increasing sugar concentration could affect adversely the osmotic conditions in the cell. This is avoided by polycondensation of glucose molecules into starch (see p. 23), a process catalyzed by transglucosidases.

In plants growing in natural habitats photosynthesis exhibits a characteristic daily cycle which essentially follows the daily course of radiation intensity. In the course of a day, therefore, assimilation starch accumulates markedly in the chloroplasts (Fig. 3.6A), to be decomposed again in the following period of darkness, mostly into sucrose, and transported in this form to the sites of utilization in the way already described (see p. 191). The starch is thus either transferred directly to the anabolism and basal metabolism (see the following chapter), where a variety of substances can be produced from it by various transformations, or it is stored, possibly after some modifications, in the storage organs as reserve materials in the form of carbohydrates, fats, or proteins (see pp. 77–79), which can be mobilized later if necessary.

All these products of the so-called primary metabolism have already been discussed in previous chapters or will be discussed in subsequent ones; a thorough treatment is therefore not necessary at this stage. The "secondary plant constituents" already referred to will, however, be considered in this context.

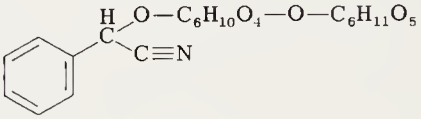
The term "secondary plant constituents" covers a large number of chemically very diverse compounds produced by the synthetic activity of plants without, however, belonging to the primary metabolism according to the present state of knowledge. The adjective "secondary" does not imply a valuation; it rather emphasizes that these materials do not occur in the plasma of every cell, but are characteristic of certain species, genera, or families. The distinction between primary and secondary materials is in any case not sharp. This would not be necessary in any case, since the term "secondary plant constituents" has no taxonomic meaning, but is only a convenient overall description.

In many cases the significance of the secondary plant constituents for the plant itself is not yet clear. Many of them may represent neutralized forms of toxic metabolic products, others may be nonutilizable metabolic end products, and some of the others could possibly be reserve materials. Many of them cause specific effects in the human and animal organism. Some of these compounds are briefly discussed below. For further details the reader is referred to the textbooks of pharmacology.

GLYCOSIDES

Glycosides are compounds of sugars with other molecules which are known as aglycons, irrespective of their chemical nature. Aglycons belong to various classes of substances, and the glycoside group therefore has a rather heterogeneous character. Strictly speaking, nucleic acids, ATP, and other compounds are all in this group, but these will be disregarded as they have already been thoroughly discussed in connection with the primary metabolism.

Amygdalin is present in all drupes, especially those of the almond tree (*Prunus amygdalus*), in bitter almonds to the extent of up to 8%. As the formula below shows, chemically the compound is benzaldehyde cyanohydrin diglycoside. The benzaldehyde and the hydrocyanic acid together give rise to the characteristic smell and taste of bitter almonds. In large quantities amygdalin is toxic, due to its hydrocyanic acid content.

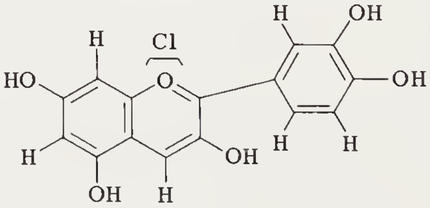


Amygdalin

Strophanthin and the digitalis glycosides, extracted from *Strophanthus* and *Digitalis* (foxglove) species, exhibit cardiotonic activity; they decrease the cardiac rate and simultaneously increase the volume circulated by one beat.

The saponins owe their name to their ability to produce copious stable foam in aqueous solution on shaking, i.e., they reduce the surface tension of water. *Saponaria alba* can contain up to 20% of saponins. Their physiological action in the cell seems to be due to their ability to react with the phospholipids at the boundary surfaces and to cause changes in their permeability. Their power to increase absorption is probably also connected with these effects.

Flavones and anthocyanins have already been discussed as pigments dissolved in the cell sap (see p. 80). Their aglycons are known as anthocyanidins, for example, the cyanidin of cornflowers (*Centaurea*) and the delphinidin of larkspur (*Delphinium*). Owing to the presence of phenolic OH groups and an oxygen atom with affinity for salt formation, the anthocyanins can form salts with both acids and bases; the former are red and the latter blue. The various red, violet, and blue hues in plant cells are, however, mainly due to the fact that the anthocyanins can exist in the form of single molecules, or as complexes with trivalent metals (Al, Fe) and a polysaccharide component as so-called chromosaccharides; the shades of color of these combinations vary.



Cyanidin chloride

Fats and Oils

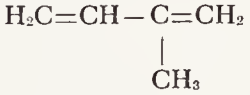
The fats have already been discussed as important reserve materials in primary metabolism. They occur in large quantities in the seeds of some higher plants. Many of them are utilized in medicine.

Castor oil is extracted from the seeds of *Ricinus communis*, which can contain up to 50% of oil. The cake left after extraction contains ricin, which is highly toxic: It agglutinates blood. Castor oil is used *inter alia* as a laxative. Ricinoleic acid glyceride is partially hydrolyzed in the intestines. Free ricinoleic acid exerts a gentle stimulating effect on the peristaltic and oscillatory movement of the intestines, while the unhydrolyzed portion supports the laxative action purely mechanically.

Croton oil, obtained from the seeds of *Croton tiglium,* is the strongest laxative known and is used only infrequently. As little as 20 drops cause choleralike diarrhea and collapse.

Terpenes

This term covers a number of compounds whose synthesis is also characteristic of plants. They are very diverse both with respect to occurrence and their properties, but they can all be derived from isoprene, C_5H_8, whether they are cyclic or not.

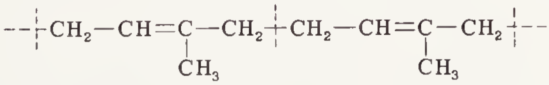


$$H_2C{=}CH{-}\underset{\displaystyle CH_3}{\underset{|}{C}}{=}CH_2$$

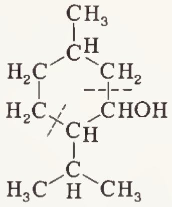
Isoprene

Their synthesis proceeds through isopentenyl pyrophosphate, i.e., a form of isoprene activated by the incorporation of pyrophosphate. The number of carbons in their molecular framework is therefore an integral multiple of five, the basic molecules having formulas of the type $C_{10}H_{16}$, $C_{15}H_{24}$, etc. Apart from the carotenoids, which have the basic formula $C_{40}H_{56}$ and which have already been discussed, phytosterols also belong to this group; among these, ergosterol is the best known. The aglycons of saponins are also terpene compounds.

Section from a latex rubber molecule



$$--\vdots CH_2{-}CH{=}\underset{\displaystyle CH_3}{\underset{|}{C}}{-}CH_2\vdots CH_2{-}CH{=}\underset{\displaystyle CH_3}{\underset{|}{C}}{-}CH_2\vdots--$$



Menthol

In view of its technical applications, rubber is one of the most important members of this group. It occurs in the chyle of many plants, but only those plants that contain a great deal of it are used as sources, e.g., *Hevea brasiliensis* and, to a smaller extent, *Ficus elastica*. The rubber macromolecules are isoprene polymers (see formula). Menthol occurs in the essential oil of peppermint (*Mentha piperita*), used widely in medicine. This also applies to eucalyptus oil, obtained from the leaves of *Eucalyptus globulus*. It has antiseptic properties and promotes blood circulation in diseased organs by a gentle stimulating action; it is therefore often used in the treatment of diseases of the mucous membranes of the mouth, throat, and nose. Camphor is obtained from the trunkwood of older camphor trees (*Cinnamomum camphora*). Camphor stimulates the respiratory and vascular centers and is therefore an excellent cardiac and respiratory stimulant for feverish diseases and also in cases of drug poisoning.

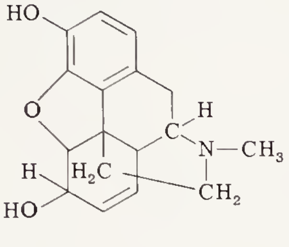
TANNINS

This name covers a chemically heterogeneous group. The characteristic properties of tannins are rather physiological and technical. They precipitate proteins and thus convert animal skins into leather. On oxidation they are transformed into the reddish-brown phlobaphenes; the dark color of many barks is due to these compounds. The best known example is tannin itself, which occurs in oak galls and in black tea. The importance of tannins for the plants is mainly due to their preservative action.

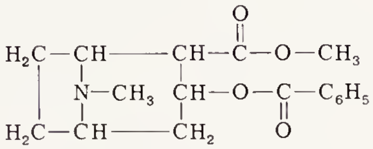
ALKALOIDS

This term is an overall one for nitrogen-containing organic bases. The chemical structure of the individual members of the group vary considerably. Many of them are used in medicine owing to their specific physiological effects. They occur in many plant groups, but are also rather characteristic of some families, e.g., the nightshade family (Solanaceae).

Morphine is the most important among the approximately 25 alkaloids present in opium which is obtained from the unripe capsules of poppies (*Papaver somniferum*); the morphine content of opium can amount to 12%. This alkaloid has a tranquillizing action on certain parts of the central nervous system and reduces the sensitivity to pain. Its analgesic effect is however combined with a euphoric one, and for this reason it is often misused. As it produces convulsions very quickly, it is one of the ost dangerous drugs. On prolonged use it tends to affect the mental ulties.



Morphine



Cocaine

Cocaine is the main alkaloid in the leaves of *Erythroxylum coca,* the "holytree" of the Incas. It paralyzes the sensory nerve endings and it was therefore once used as a local anesthetic. Recently it has been replaced by other products, as it is one of the most widespread narcotics. It represses the symptoms of tiredness and exhaustion and therefore helps to achieve outstanding physical performance. The actual capacity of the body is, of course, not increased so that total collapse follows rapidly.

Quinine, found in the bark of the cinchona tree (*Cinchona succirubra*), kills the merozoites of malaria pathogen (*Plasmodium malariae*) and prevents the bouts of fever. Nicotine is the alkaloid of tobacco (*Nicotiana tabacum*). Ergot of rye (*Secale cornutum*), i.e., the sclerotium[6] of the fungus *Claviceps purpurea,* contains among other substances, many alkaloids, e.g., ergotamine and ergotoxine. These cause an increase in the rate and intensity of rhythmic uterine contractions; ergot extracts are therefore used in obstetrics.

Caffeine, found in the coffee bean (the seeds of the coffee tree) (*Coffea arabica*) and elsewhere, is, strictly speaking, not an alkaloid but a purine.

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[6] This term is used to describe the resistant organs of many fungi. They consist of a thick mycelium reticulum and are surrounded by a robust sheath. The mycelium of *Claviceps purpurea* penetrates the embryonic nodes of flowering rye plants. When these tissues have all been used up, the mycelium forms a black, crescent-shaped sclerotium. This is known as ergot.

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Chapter 11

Respiration and Energy Transformations

Photosynthesis is a process in which hydrogen is separated from oxygen and is fixed in the form of a metastable carbon compound. All organisms make use of the energy gap which thus arises between hydrogen and oxygen: They oxidize the carbon compounds and utilize their energy. This occurs whether or not the organism is autotrophic, i.e., whether or not it has synthesized the carbon compound itself. In the typical case, i.e., in the presence of elemental oxygen, this process continues until the potential is completely dissipated and the hydrogen and oxygen are recombined to water; simultaneously, the CO_2 which has served as a hydrogen carrier and which is no longer required for this purpose is released. The overall equation for this reaction shows that it is in a way a reversal of photosynthesis.

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 675 \text{ kcal}$$

This process is therefore exergonic, as the whole amount of energy which was built into the carbohydrate is released again, and is described as *respiration* or dissimilation. The large quantity of energy is not released instantaneously but in stages, so that respiration can be regarded as a process of controlled oxidation of hydrogen, which supplies the organisms with the energy necessary for their life processes.

According to the theory put forward by H. Wieland in 1912, the primary act of respiration is *dehydrogenation*, i.e., cleavage of hydrogen away from the respiratory substrate, which is thus oxidized. The hydrogen need not be transferred directly to oxygen, as other substances can also act as hydrogen acceptors. The end product in this case is therefore not water but another organic compound, which still has a relatively high energy content. Such energy-releasing processes which usually proceed under anaerobic conditions are known as *fermentations*. As has already been pointed out in the discussion of chemosynthesis, the term *oxidation* refers not only to combination with oxygen but also to dehydrogenation or to removal of electrons.

BASIC EXPERIMENT

Biological oxidation is a relatively complicated sequence of reactions whose course has only been clarified to some extent by research carried out in the last few decades. However, the reactants appearing in the overall equation given above can be identified by relatively simple experiments, though water once more constitutes an exception.

Demonstration of the Utilization of Oxygen

Some germinating seeds (e.g., peas) are kept over a long period in a closed cylinder. If a burning candle is introduced into the cylinder, the flame is extinguished at once, as no oxygen is left under the cylinder.

Demonstration of the Liberation of Carbon Dioxide

Air is freed from carbon dioxide by bubbling it through a concentrated sodium hydroxide solution and is then passed through a washbottle into which seeds have been placed. The air picks up carbon dioxide in the washbottle, which can be identified by bubbling the air through a barium hydroxide solution and observing the precipitation of barium carbonate.

If these experiments are carried out with parts of green plants they must be conducted in the dark to avoid the superimposed effect of photosynthesis. The amount of oxygen used and CO_2 released can, of course, be measured by means of the exact methods mentioned in the preceding chapter. The respiratory quotient CO_2/O_2 can be calculated from the results obtained; for carbohydrates, according to the overall equation given above, this value is equal to unity. If compounds poor in oxygen (e.g., fats) are oxidized this quotient is smaller than unity, while the oxidation of the relatively oxygen-rich carboxylic acids gives a value greater than unity.

Demonstration of the Release of Energy

Plants do not utilize the whole of the energy becoming available in the course of biological oxidation; part of it is dissipated as heat. This can be shown by letting some seeds germinate in a Dewar flask. The temperature rise on germination can amount to several degrees centigrade. This energy loss, which manifests itself as body warmth in animal organisms, cannot be observed in plants without special equipment, as the plants' large surface area allows a rapid exchange of heat with the surroundings, resulting in thermal equilibrium.

The Oxidative Breakdown of Carbohydrates

The whole process can easily be subdivided into several subsections which will be discussed separately for the sake of clarity. These subsections are as follows: (1) Glycolysis: Cleavage of the glucose molecule into smaller units with removal of hydrogen, which leads to the formation of pyruvic acid; (2) oxidative decarboxylation of pyruvic acid leading to the formation of C_2 compounds; (3) citric acid cycle: complete decomposition of the C_2 compounds with stepwise elimination of hydrogen and carbon dioxide; (4) terminal oxidation: combination of the hydrogen split off with oxygen in the respiratory chain, accompanied by stepwise release of energy and formation of energy-rich phosphates.

The oxidative breakdown of carbohydrates is one of the best investigated biochemical processes, for which comprehensive data are available, but all this cannot be treated here in detail. The discussion will rather be limited to the questions of how the carbohydrate molecule is broken down and how the resulting energy is utilized. Many enzymes take part in these reactions; the action of these is now mostly well understood. All enzymes taking part shall not be named, however, again for the sake of clarity. Interested readers should consult the relevant textbooks of biochemistry.

Glycolysis

The basic substances of biological oxidation are the hexoses, especially glucose and fructose. Other carbohydrates, e.g., the polysaccharides, must first be transformed into glucose. This is achieved either by phosphorolysis or by hydrolysis.

The more frequently followed path, which is also more advantageous for the plant, is phosphorolysis. In this process, the molecules of starch (and of other polysaccharides too) are degraded starting from the nonreducing end (see p. 23) with the aid of the enzyme phosphorylase and react with phosphate to form glucose-1-phosphate. This is transformed into glucose-6-phosphate which can undergo glycolysis directly (see below).

In some cases, i.e., during the mobilization of reserve starch in seeds, the decomposition can, however, proceed also with the aid of amylases. Two types of amylases are known. α-Amylase attacks first the interior of the starch molecule, and splits it into smaller units containing 6–7 glucose molecules each. β-Amylase, on the other hand, decomposes starch or its cleavage products from the nonreducing end (Fig. 11.1) by repeatedly cleaving off maltose molecules. By analogy with the peptidases, (see p. 243) they can also be regarded as *endo-* and *exo*-amylases. The end product of this hydrolysis type of starch degradation is maltose, which is decomposed into glucose units by the action of maltase. Before it can undergo glycolysis, the glucose must then be phosphorylated in the C-6 position in the way already described (see p. 195).

During glycolysis, the glucose-6-phosphate is transformed into fructose-1,6-diphosphate by a further phosphorylation in the C-1 position. The latter is cleaved by the action of the aldolase into two triose phosphate molecules, dihydroxyacetone phosphate and glyceraldehyde-3-phosphate (see the glycolysis reaction scheme). Glycerolaldehyde-3-phosphate is then oxdized to 3-phosphoglyceric acid, and the energy released in this process is partially taken up by ATP (substrate chain phosphorylation). The hydrogen split off is taken up by NAD$^+$, which

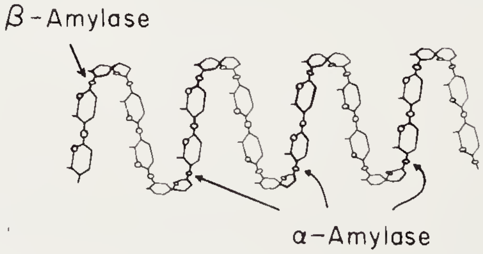
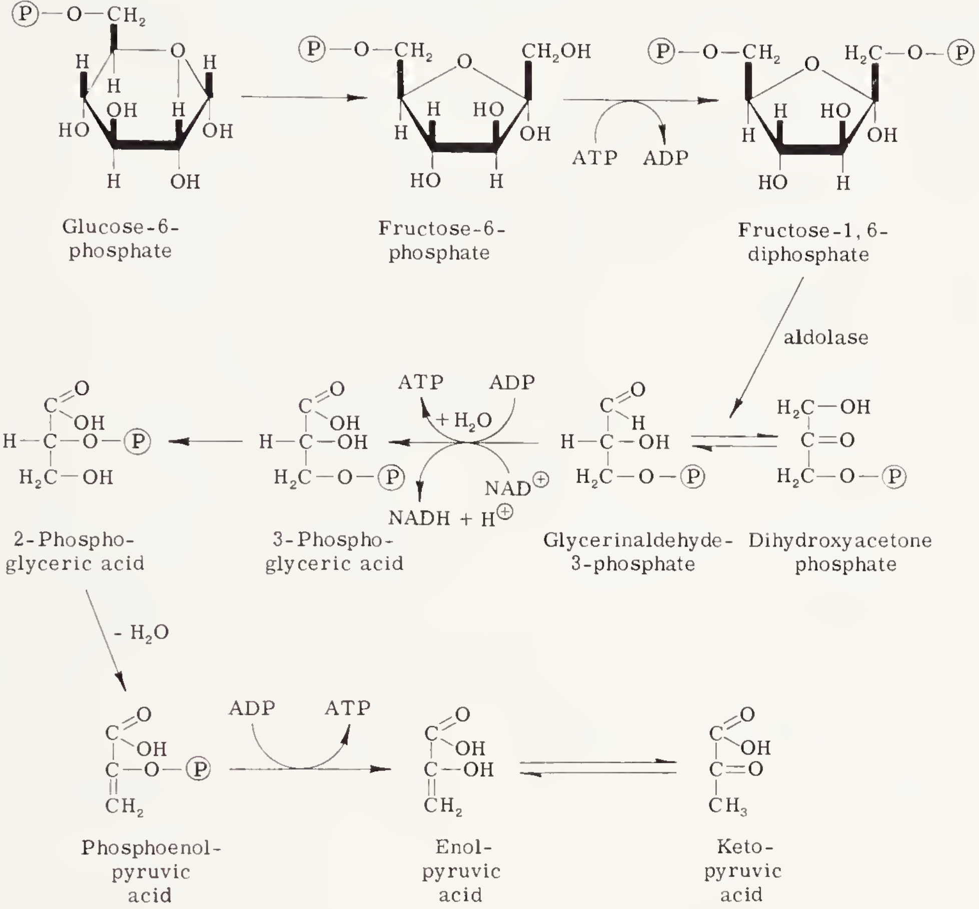


FIG. 11.1. Schematic action of α- and β-amylases.



Glycolysis

is correspondingly transformed into NADH+H$^+$. Finally, phosphoenolpyruvic acid is formed via 2-phosphoglyceric acid and with elimination of water; the phosphate radical is taken up by ADP which is hence transformed into ATP. The ATP used for the phosphorylation of glucose is thus regenerated. The enolic form of pyruvic acid is then transformed into the keto form. Pyruvic acid represents a central point in cell metabolism through which the course of the dissimilation process proceeds. We shall return later to this subject; first, however, the process of oxidative decomposition will be pursued further.

THE CITRIC ACID CYCLE

The pyruvic acid is transformed into an acetyl radical ($H_3C-C=O$) by an oxidative decarboxylation in which hydrogen and a molecule of CO_2 are cleaved off. This acetyl radical is taken up by coenzyme A (known as CoA or as CoA-SH, since it carries an SH group), which is thereby transformed into acetyl-CoA. The hydrogen is taken up by NAD^+. The acetyl-CoA then transfers the acetyl radical to oxalacetic acid (four carbons), converting it into citric acid (six carbons). CoA is thereby regenerated and is ready to take up another acetyl radical.

The acetyl radical built into the citric acid molecule is totally decomposed by repeated release of hydrogen and carbon dioxide; finally the oxalacetic acid is regenerated by this process. This cycle is known as the citric acid cycle, tricarboxylic acid cycle, or as the Krebs[1]-Martius cycle after its discoverers. The intermediate steps of the cycle are shown in the diagram. Every acetyl radical gives rise to two CO_2 molecules, which together with the one released during the oxidative decarboxylation gives 3 CO_2 molecules per molecule of triose phosphate amounting to six molecules of CO_2 per molecule of glucose. The oxidation therefore does not occur with elemental oxygen but proceeds according to Wieland's dehydrogenation scheme, i.e., water is taken up and hydrogen is eliminated. The four pairs of H atoms are taken up by the coenzymes NAD^+ and FAD, giving four reduced coenzymes. Together with the two reduced coenzymes produced in the oxidation of glyceraldehyde and in the oxidative decarboxylation, the numbers of reduced coenzymes formed per molecule of triose and glucose are 6 and 12 respectively. The overall equation for glycolysis and the citric acid cycle is therefore:

$$C_6H_{12}O_6 + 6H_2O + 12 \text{ coenzymes} \rightarrow 6CO_2 + 12 \text{ coenzymes-}H_2$$

The amount of energy released in the citric acid cycle is relatively small, as only one energy-rich phosphate, in this instance GTP (see p. 196) is formed for each acetyl radical. This shows that the bulk of the energy released in respiration is not due to the "combustion" of carbon to carbon dioxide. The main task of the citric acid cycle, into which the decomposition of fats and proteins is also channeled via acetyl-CoA, is rather to transform all materials decomposed for the release of energy irrespective of their chemical nature into a homogeneous energy source, the reduced coenzymes; further utilization of these will be discussed in the next section.

It must be pointed out in this context that some intermediate products produced in the citric acid cycle serve as starting materials for the synthesis of other important compounds, e.g., certain amino acids (see p. 240). In plants utilizing fats as reserve materials (see p. 79) and

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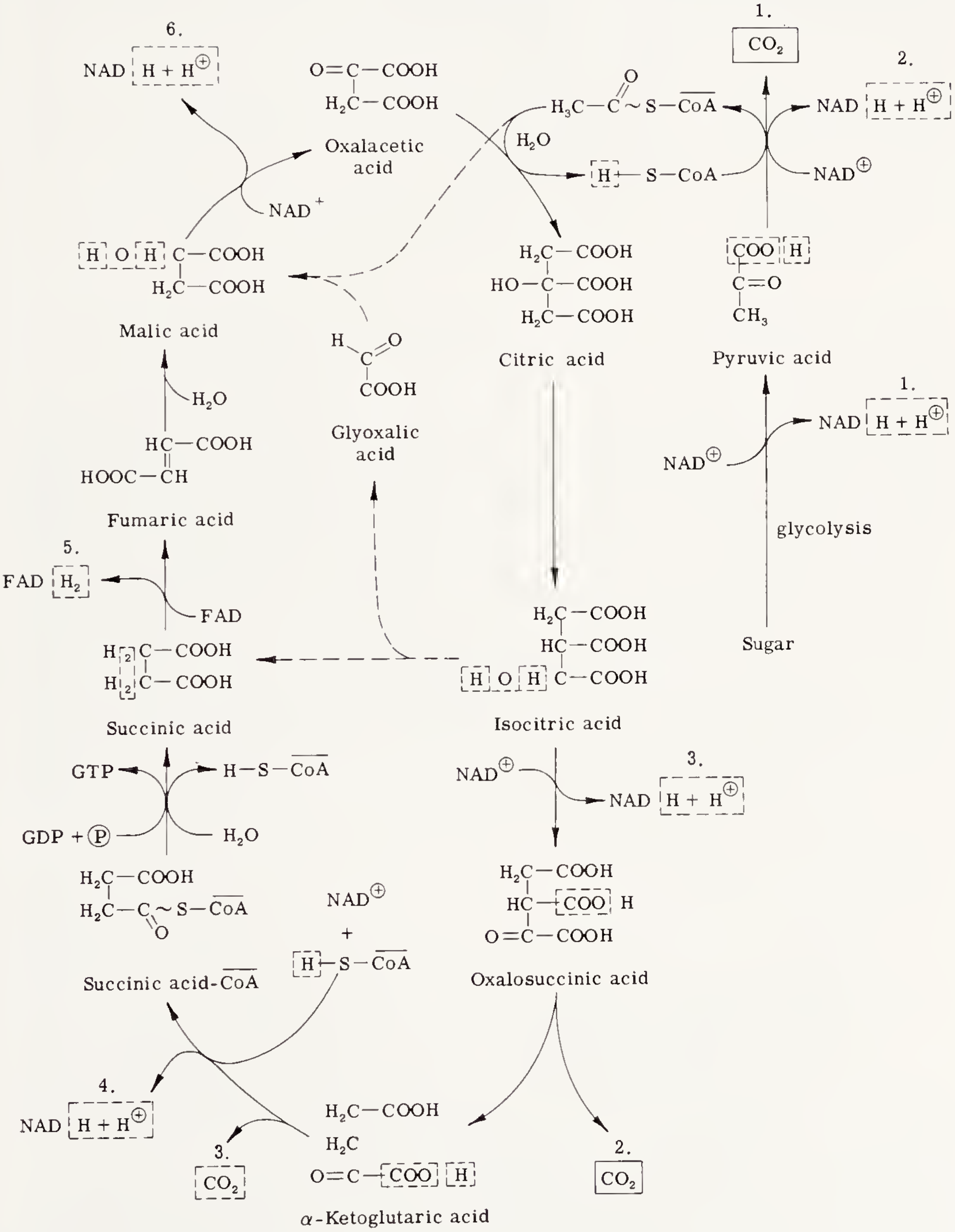
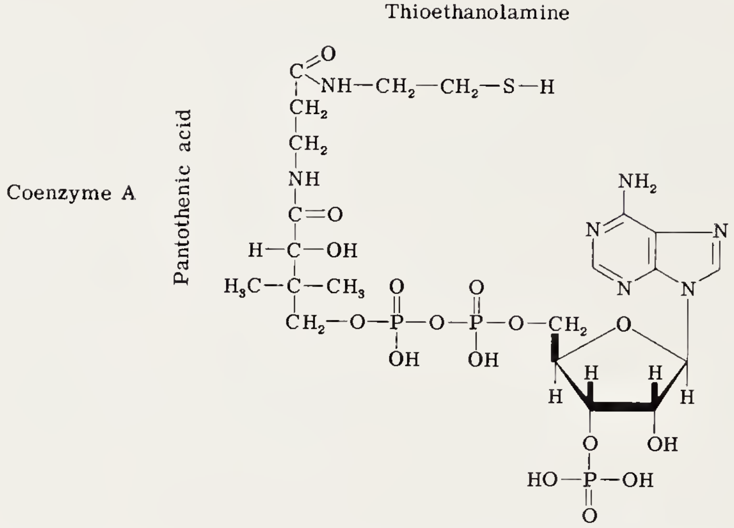
[1] H. A. Krebs received the 1953 Nobel prize for medicine for this work.

The citric acid cycle
(the broken arrows indicate the glyoxalic acid cycle)





also in certain microorganisms utilizing acetic and other fatty acids, some of these intermediate compounds are formed in the so-called glyoxalic acid cycle. This is to some extent short-circuiting the citric acid cycle (see scheme), in the succinic acid (C_4) and glyoxalic acid (C_2) are formed directly by cleavage of isocitric acid (C_6). The glyoxalic acid condenses with acetyl-CoA to yield malic acid. Further transformations of succinic and malic acid yield oxalacetic acid; glucose can be formed from the latter in a process which corresponds approximately to reversed glycolysis. The transformation of reserve fats into carbohydrates for long-range transport (see p. 191) may also proceed in this way.

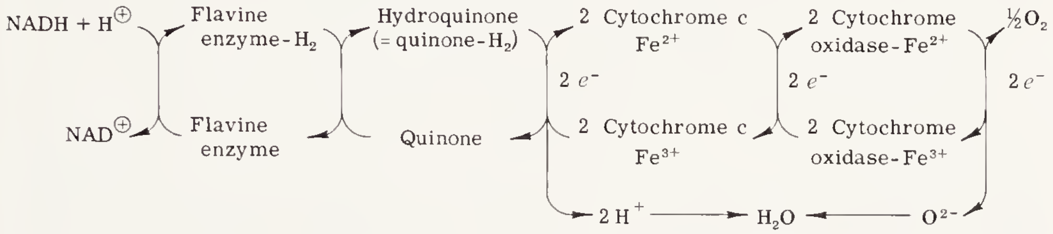
Terminal Oxidation

The combination of hydrogen with oxygen to form water occurs in the respiratory chain. The hydrogen is provided mainly by $NADH+H^+$ and to a smaller extent by $FADH_2$.

The reaction of hydrogen with oxygen releases a relatively large quantity of energy; it therefore occurs in several coupled stages, whose details are still somewhat obscure. The following discussion will consequently be limited to the essentials.

The $NADH+H^+$ is oxidized by flavine enzymes, the active groups of which are mostly flavine-adenine dinucleotide (FAD) (see p. 199); the flavine enzyme itself is reduced to FAD-H_2. The two hydrogen atoms are then transferred, as shown in the diagram below, to quinone, or most often probably to ubiquinone (coenzyme Q) which is thereby transformed into hydroquinone. This ends the transport process of hydrogen atoms, which are released from the hydroquinone as H^+ ions. The electrons released at the same time are taken up by cytochrome c.

Schematic diagram of the respiratory cycle



The active group of the cytochromes is the porphyrin ring system, the basic structure of which has already been discussed in connection with chlorophyll. The center of the ring is occupied by an iron atom (in chlorophyll a magnesium atom is found in the same position), which can take up an electron while changing its valence: $Fe^{3+} + e^- \rightarrow Fe^{2+}$. Various cytochromes have been identified, known as cytochrome a, b, and c. Cytochrome a is identical with cytochrome oxidase, Warburg's respiratory enzyme.

It is still uncertain whether cytochrome b is also directly connected with electron transport. The last link of the chain is in every case cytochrome oxidase; this finally transfers the electrons to elemental oxygen. The oxygen atom is converted into an ion by the uptake of two electrons, and the oxygen ion finally combines with two hydrogen ions to form water. This is the last step in the biological oxidation process.

The overall equation for the oxidative degradation of carbohydrates, which can be derived from the equations of glycolysis and the citric acid cycle, on the one hand, and from the terminal oxidation, on the other, is as follows:

$$\begin{array}{lcl}
C_6H_{12}O_6 + 6H_2O + 12 \text{ coenzymes} & \rightarrow & 6CO_2 + 12 \text{ coenzymes-}H_2 \\
12 \text{ coenzymes-}H_2 + 6O_2 & \rightarrow & 12 \text{ coenzymes} + 12H_2O \\
\hline
C_6H_{12}O_6 + 6O_2 & \rightarrow & 6CO_2 + 6H_2O
\end{array}$$

As has already been mentioned, each transition from one step to the next releases a certain amount of energy, as the energy of the consecutive members decreases along the respiratory chain. A large part of this energy is stored in the energy-rich bonds of ATP, where it is available for use in other metabolic processes. This process of ATP formation, which is bound up with the respiratory chain and which represents its energy-releasing section proper, is known as respiratory chain phosphorylation. It has been found that approximately 3 moles of ATP are formed for every mole of water formed; this represents an energy yield of about 21 kcal. The formation of free water releases about 57 kcal/mole, so that the efficiency of biological carbohydrate oxidation is about 40%, when it is taken into account that hydrogen in NADH+H^+ already has a somewhat lower energy than molecular hydrogen.

The oxidation of NADH+H^+ is coupled with ATP synthesis, and it can therefore proceed only if sufficient ATP is available, i.e., a corresponding amount of ATP must be used up. The cell can thus control the oxidation process. When work is done by the cell, ATP is used up and ADP is formed; this causes oxidation of the reduced coenzymes. When the ATP consumption is low, the rate of coenzyme oxidation is also reduced. Such an arrangement is described as a *feedback system.*

Both the enzymes of the citric acid cycle and of the respiratory chain are found in the mitochondria (see p. 43). It seems that a lipoprotein enzyme and a water-soluble protein enzyme alternate in the respiratory chain, and it is therefore assumed that the individual members are arranged in a definite sequence in the lipoprotein membranes of the mitochondrial cristae and tubuli. A definite steric arrangement of enzymes is certainly essential for proper functioning of a mechanism as complicated as the respiratory chain.

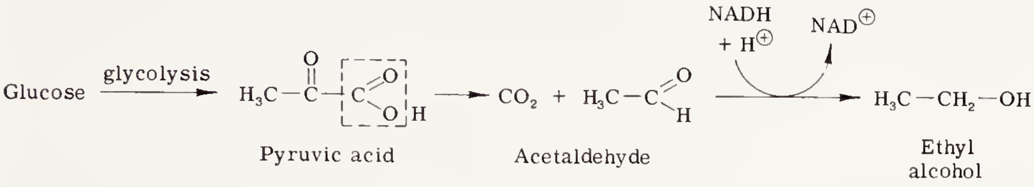
Fermentation

It has already been mentioned (see p. 224) that substances other than oxygen can also act as hydrogen acceptors; such is the case in fermentation processes. The end products of these processes are relatively rich in energy and are very variable, depending on the type of substance utilized as the hydrogen acceptor. The fermentations are named after their end products. Thus the product of alcoholic fermentation is ethyl alcohol, that of lactic acid fermentation is lactic acid, etc. Fermentation processes are, as a rule, anaerobic.

ALCOHOLIC FERMENTATION

This process takes place largely along the same lines as glycolysis, which has already been discussed, and it can easily be derived from glycolysis.

Historically, the development occurred the other way round, as alcoholic fermentation was the first biochemical process to be fully understood. Only much later has it been recognized that the first steps of biological oxidation proceed in the same manner.



Alcoholic fermentation

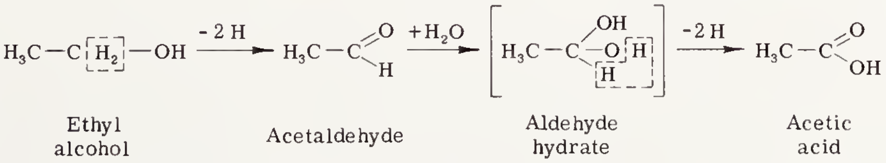
Alcoholic fermentation is effected by yeasts, e.g., brewer's yeast (*Saccharomyces cerevisiae*). The substrate is again glucose; the decomposition of this compound to pyruvic acid follows the same path as in glycolysis. Pyruvic acid is next decarboxylated to yield acetaldehyde, rather than entering the citric acid cycle. The acetaldehyde is reduced to ethyl alcohol by NADH+H+, which is produced by the oxidation of glyceraldehyde-3-phosphate.

$$C_6H_{12}O_6 \rightarrow 2CO_2 + 2C_2H_5OH + 21\ \text{kcal}$$

The amount of energy released is small, corresponding to the anaerobic nature of the process. Two moles of ATP are produced per mole of glucose. The yeasts must therefore decompose considerable amounts of glucose to cover their energy requirements, and this leads to rapid accumulation of the alcohol. However, yeasts are also capable of performing oxidative breakdown. They are therefore facultative anaerobes, and can thrive in the presence of oxygen.

Oxidation of Alcohol

Corresponding to the small energy release in the alcoholic fermentation process, ethyl alcohol is a rather energy-rich compound which can be further oxidized by other organisms to release more energy. *Azotobacter* species can be mentioned as examples: These oxidize ethyl alcohol to acetic acid, as shown by the following reaction sequence. The process is another example of Wieland's dehydrogenation scheme.



Oxidation of alcohol to acetic acid

First, alcohol is dehydrogenated to yield acetaldehyde. The latter takes up water to form an unstable hydrate, which gives acetic acid on further dehydrogenation. The hydrogen released is then transferred to oxygen via the coenzymes, probably the cytochrome system. The amount of energy released is accordingly high.

$$C_2H_5OH + O_2 \rightarrow CH_3COOH + H_2O + 118 \text{ kcal}$$

The acetic acid fermentation, which is also used industrially for the production of vinegar from wine, is therefore an aerobic process.

LACTIC ACID FERMENTATION

This process is also identical to glycolysis up to the pyruvic acid stage. However, the pyruvic acid is not decarboxylated to acetaldehyde as it is in alcohol fermentation. There is therefore no evolution of gas. Pyruvic acid itself serves here as a hydrogen acceptor, and is transformed into lactic acid by the uptake of hydrogen that has been released in glycolysis and transferred by means of $NADH+H^+$.

$$H_3C\text{–}CO\text{–}COOH + [NADH + H^+] \rightarrow H_3C\text{–}CHOH\text{–}COOH + NAD^+$$

The overall equation for lactic acid fermentation can be written as

$$C_6H_{12}C_6 \rightarrow 2CH_3\text{–}CHOH\text{–}COOH + 22 \text{ kcal}$$

The energy yield of this process is also low, corresponding to its anaerobic nature. Two moles of ATP are produced per mole of glucose as in alcoholic fermentation. Many bacteria are capable of performing lactic acid fermentation. The "pure" lactic acid producers include *Streptococcus lactis* and some species of the genus *Lactobacillus,* e.g., the yogurt organism, *L. bulgaricus,* which play a role in milk processing and in the industrial production of lactic acid.

FURTHER FERMENTATIONS

In addition to those discussed above, there are a number of other fermentation processes, e.g., the fermentation of propionic acid, and butyric acid, which are performed—sometimes simultaneously—by a variety of bacteria. The butyric acid producers include the ubiquitous *Clostridium pasteurianum;* especially noteworthy *Clostridium* species are the pathogens of gas gangrene and anthrax: These owe their names to the pronounced evolution of CO_2 and H_2 during the production of butyric acid.

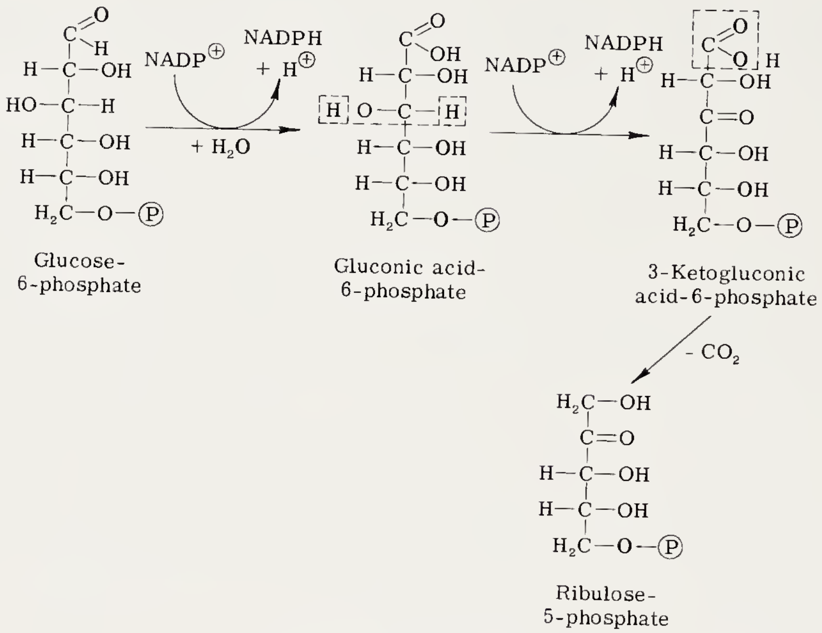
It must be mentioned in this context that higher plants can also derive energy from anaerobic processes. If the supply of atmospheric oxygen is cut off, plants can continue to "breathe" which can be proved by identifying the CO_2 produced. This can be done by placing swollen seeds, e.g., peas, in a test tube fully filled with mercury; the lower end of the test tube is immersed in a dish of mercury. The mercury column is soon depressed by the evolving gas. The gas can be identified as CO_2 by adding sodium hydroxide: The CO_2 is absorbed and the mercury rises again. Both the ethyl alcohol and the lactic acid produced can also be identified in the tissues of anaerobically breathing plants. This process was previously known as intramolecular respiration to emphasize that the process is only one of intramolecular rearrangement. The application of the term "fermentation" is, however, fully justified here.

ANAEROBIC RESPIRATION

Some microorganisms are even capable of performing the oxidative decomposition of carbohydrates anaerobically, i.e., in the absence of elemental oxygen, by utilizing oxygen in inorganic combinations as the hydrogen acceptor. Many of them use nitrates or nitrites which they reduce to nitrous oxides (N_2O) or even to elemental nitrogen. This denitrification process results in the breakdown of nitrates in poorly aerated soils which are thus lost as plant nutrients. Other organisms can reduce sulfates. The reduction produces hydrogen disulfide, often in large quantities.

Direct Oxidation of Glucose

Apart from the decomposition of glucose in glycolysis and in the citric acid cycle, there is a further possibility, namely the direct oxidation of glucose. In this process as shown by the reaction sequence above, glucose-6-phosphate is dehydrogenated by $NADP^+$, with the uptake of water, giving rise to gluconic acid-6-phosphate. This is again dehydrogenated by $NADP^+$ and forms 3-ketogluconic acid-6-phosphate. By decarboxylation, the latter gives rise to ribulose-5-phosphate, a C_5 compound. Six molecules of ribulose-5-phosphate can again yield five glucose



Direct oxidation of glucose

molecules in the so-called pentose phosphate cycle which is somewhat similar to the Calvin cycle (see p. 211) discussed in connection with photosynthesis but running in the opposite direction. The overall equation can be written:

$$\begin{array}{r}
6\ \text{glucose-6-phosphate} + 12\ \text{NADP}^+ + 6\text{H}_2\text{O} \rightarrow 6\text{CO}_2 + 12[\text{NADPH} + \text{H}^+] \\
+\ 6\ \text{ribulose-5-phosphate} \\
6\ \text{ribulose-5-phosphate} \rightarrow 5\ \text{glucose-6-phosphate} \\
\hline
1\ \text{glucose-6-phosphate} + 12\ \text{NADP}^+ + 6\text{H}_2\text{O} \rightarrow 6\text{CO}_2 + 12[\text{NADPH} + \text{H}^+]
\end{array}$$

Finally, this process also produces 6 molecules of CO_2 and 12 reduced coenzymes from one molecule of glucose. In contrast, however, to glycolysis and the citric acid cycle, only $NADPH+H^+$ is produced here. Before it can enter the respiratory chain, hydrogen must be transferred to NAD^+.

$$[\text{NADPH} + \text{H}^+] + \text{NAD}^+ \rightarrow \text{NADP}^+ + [\text{NADH} + \text{H}^+]$$

This, however, seems to occur only to a limited extent, so presumably the purpose of the hydrogen released during direct oxidation of glucose is not so much to provide energy but rather to be available for syntheses involving reduction. Direct oxidation of glucose must therefore be regarded as a secondary path; the bulk of the transformations take place along the path of oxidative decomposition.

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Chapter 12

Nitrogen Metabolism

The discussion so far has been limited essentially to the metabolism of carbohydrates, whose function is partly the provision of energy and partly synthesis of specific compounds. However, it has already been explained that the body of plants at the molecular level consists of a number of organic nitrogen compounds, such as the proteins and the purine and pyrimidine components of nucleotides, which are essential to the vital processes. The object of this chapter is to describe the synthesis and breakdown of these compounds.

The Source of Nitrogen

Just as in the case of carbon nutrition, plants can be divided into autotrophic and heterotrophic forms; the former can utilize nitrogen in inorganic combination, or even elemental nitrogen, while the latter rely on organic nitrogen compounds.

It has already been mentioned in the discussion of ion uptake that green plants are autotrophic not only with regard to carbon but normally also with regard to nitrogen. Nitrogen is taken up preferentially in the form of the NO_3^- ion from the soil, which is therefore the most important, often even the sole source of nitrogen for the higher plants. As a rule, NO_3^- can be replaced by NH_4^+, but the continued uptake of NH_4^+ presents many higher plants with difficulties owing to the concomitant acidification of the soil (see p. 189). Since nitrogen occurs in most soils only in relatively small quantities it is the limiting factor), it must be replaced from time to time by applying fertilizers to intensively cultivated soils. The amounts of nitrogen oxides produced by electric discharges in the atmosphere and transferred to the soil by rainwater are small.

FIXATION OF ELEMENTAL NITROGEN

The elemental nitrogen dissolved in soil moisture can be fixed by certain bacteria, especially by the Actinomycetes, and also by many Cyanophyceae. These either live freely in the soil or are symbiotic (see p. 251) with higher plants. The unattached bacteria include Actinomycetes like *Azotobacter chroococcum* and *Clostridium pasteurianum;* the former is aerobic while the latter is anaerobic. The Cyanophyceae also live freely in the soil. The amount of nitrogen fixed by these organisms taken as a whole is quite significant (20–40 kg per hectare per annum) and is not a negligible factor in the nitrogen balance of the soil.

Among the symbiotic nitrogen-fixing organisms, the ones most important in practice are the root tubercle bacteria of leguminous plants (see p. 252). These enable plants to thrive even on soils poor in nitrogen. Similar tubercles containing Actinomycetes as symbionts occur on the alder (*Alnus glutinosa*). There are also symbionts among the nitrogen-fixing Cyanophyceae.

The Incorporation of Nitrogen

The nitrogen must first be reduced to NH_3, irrespective of whether the original source is elemental nitrogen or the NO_3^- ion.

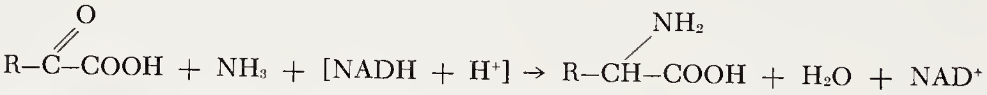
The hydrogen required for the reduction of elemental nitrogen is supplied by organic hydrogen donors. The reduction is coupled with respiration. In the photoautotrophic species among the nitrogen-fixing organisms, such as the purple bacteria and the Cyanophyceae, the reduction equivalents $NADPH+H^+$ produced during photosynthesis are probably mainly used for the reduction of nitrogen. The first step in the nitrate reduction yields nitrate. This process, in which both NADPH $+H^+$ and often also $NADH+H^+$ may act as hydrogen donors, is catalyzed by nitrate reductase, which so far has been identified in all plants analyzed for the purpose. Cofactors (FAD, molybdenum) also take part in the reaction, but their action cannot be discussed here in detail. Further reduction proceeds to hydroxylamine (NH_2OH) through intermediate, still obscure, steps and thence to ammonia.

SYNTHESIS OF AMINO ACIDS

While animals can synthesize only part of their amino acid requirements, and must receive the remaining (so-called essential) amino acids in their diet, plants are normally able to synthesize all the amino acids that they require.

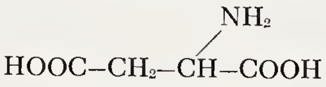
The paths of synthesis vary greatly, depending on the particular amino acid synthesized. They proceed through many intermediate steps, which cannot be discussed here in detail. Only some simple examples will be given in the following section.

One important pathway is the *reductive amination* of α-keto acids; as has already been discussed, (see pp. 227, 229), these are formed both in glycolysis and in the citric acid cycle. This reductive animation process consists of the production of ammonia with elimination of water and simultaneous reduction by $NADH+H^+$; finally, amino acids are formed. The overall reaction sequence follows.



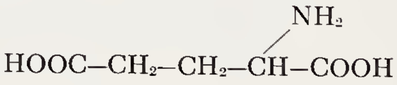
$$R\text{–}\overset{O}{\overset{\|}{C}}\text{–}COOH + NH_3 + [NADH + H^+] \rightarrow R\text{–}\overset{NH_2}{\overset{|}{C}H}\text{–}COOH + H_2O + NAD^+$$

In this type of reaction oxalacetic acid can be transformed into aspartic acid and α-ketoglutaric acid into glutamic acid.



$$HOOC\text{–}CH_2\text{–}\overset{NH_2}{\overset{|}{C}H}\text{–}COOH$$

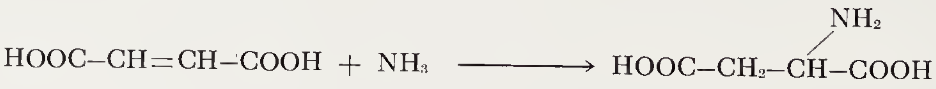
Aspartic acid



$$HOOC\text{–}CH_2\text{–}CH_2\text{–}\overset{NH_2}{\overset{|}{C}H}\text{–}COOH$$

Glumatic acid

Another process leads to the same products but from unsaturated dicarboxylic acids, e.g., from fumaric to aspartic acid by the addition of NH_3 to the double bond.

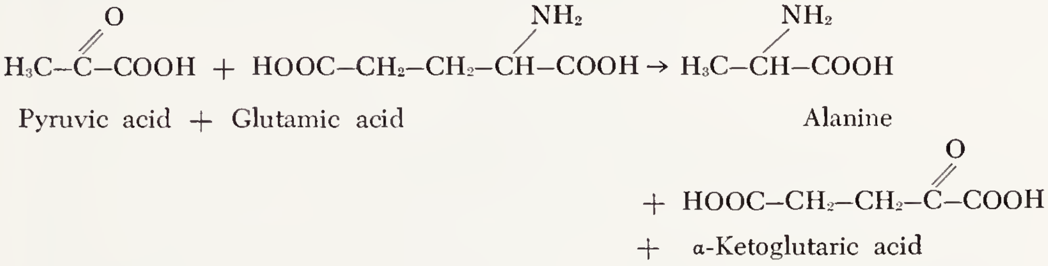


$$HOOC\text{–}CH{=}CH\text{–}COOH + NH_3 \longrightarrow HOOC\text{–}CH_2\text{–}\overset{NH_2}{\overset{|}{C}H}\text{–}COOH$$

Fumaric acid

Aspartic acid

A third path of amino acid synthesis is *transamination;* in this, NH_2 groups are transferred from an amino acid to an oxy or keto acid, as shown in the following example.



The amino-group donor in this reaction is glutamic acid. This process is catalyzed by transaminases which contain pyridoxal phosphate (vitamin B_6, see p. 325) as a prosthetic group. The synthesis of other amino acids will be discussed later.

PROTEINS

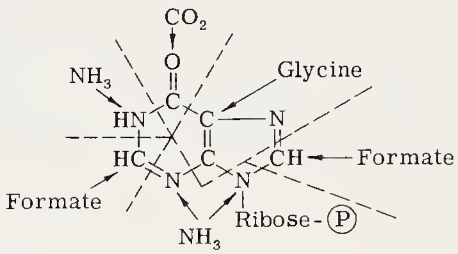
As has already been explained (see p. 16), proteins consist of a large number of amino acids combined through peptide linkages. The formation of a peptide link between an amine group and a carboxyl group with the elimination of water is a relatively complicated process which is by no means completely understood. The problem of the combination of individual amino acids is connected with the question of maintenance of a certain amino acid sequence; the biosynthesis of proteins will therefore be discussed later (see pp. 311–314).

The main sites of amino acid synthesis in higher plants are in the leaves. This emphasizes the close connection between carbohydrate and protein metabolism.

SYNTHESIS OF NUCLEIC ACIDS

The synthesis of neucleotide bases, the purines and pyrimidines, is, like that of the cyclic amino acids, a stepwise process which will not be described here in detail. Clarification of the synthetic process has shown that the nucleotide bases are not formed by the reaction of increasingly more complicated intermediate products as has been assumed at one time, but that they are synthesized from relatively simple molecules like glycocoll, formic acid, CO_2, and NH_3 without interruption. At first

NH_3 is incorporated into amino groups in the way just described, and it is then transferred (aspartic and glumatic acid).



Components of the purine ring

The diagram shows a purine ring as an example in which the provenance of each group is indicated. The whole synthesis is based on the ribose or deoxyribose phosphate molecule, which is available at the start of the process and which acts as a nucleus for it. Details of the combination of individual nucleotides with one another will be given later (see p. 297).

OTHER NITROGENOUS COMPOUNDS

Nitrogen has been recognized as a component of many more compounds which take part in the nitrogen metabolism in plants, e.g., in the pyrrole nuclei of the porphyrin rings of chlorophyll and of cytochrome, in growth substances (see p. 343), and in the alkaloids. Discussion of the incorporation of nitrogen into these compounds and of their syntheses is outside the scope of this book.

Degradation of Nitrogenous Compounds

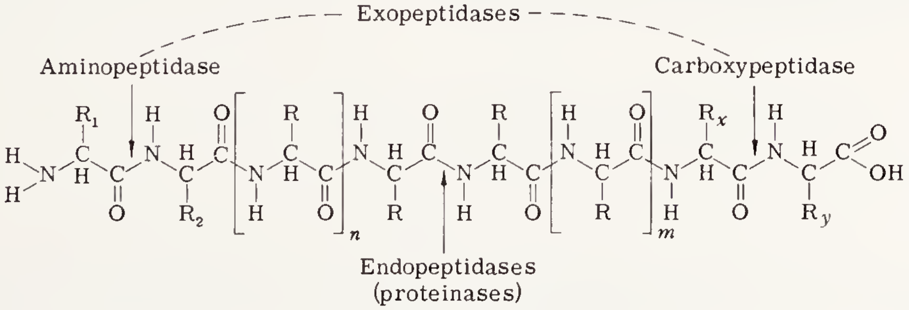
The discussion of the breakdown of nitrogenous compounds is again mainly concerned with proteins and amino acids. The constant synthesis of proteins is accompanied by a steady protein breakdown, as proteins built into the plasma structures do not remain in there forever but are displaced after some time by freshly synthesized molecules (see p. 32). In heterotrophic organisms, which utilize proteins as nutrients, the proteins must first be broken down into their components before they can be used for the synthesis of species-specific proteins, if they are not used as a source of energy and thus completely decomposed (see p. 244). In all plants using proteins as reserve materials (see p. 78) the mobilization of the reserve materials is bound up with protein breakdown; every transport process within the plant also requires transformation of proteins into amino acids.

DEGRADATION OF PROTEINS

Inspection of the reaction equilibrium of peptide formation from two amino acids given on p. 16 shows that the equilibrium is shifted strongly to the left, i.e., to the side of the amino acids. Peptide synthesis therefore requires the addition of energy. The reverse reaction, hydrolysis of the peptide linkage, can, of course, proceed without the addition of energy (on the contrary, a certain quantity of energy is thereby released, though this does not seem to be utilized by the organisms).

The degradation of proteins is catalyzed by proteases which, by definition, belong to the hydrolase group. The proteolytic enzymes were discovered relatively early, and several extracts have been prepared, e.g., papain from the chyle of papaya (*Carica papaya*) or pepsin and trypsin, from the digestive juices of animals. These were, however, mostly enzyme mixtures.

Endo- and exopeptidases can be distinguished according to the mode of action of the enzymes on protein and peptide chains. As can be seen from the following diagram, the endopeptidases (also known as proteinases) attack the middle of longer peptide chains and split them into low-molecular peptides. On the other hand, exopeptidases degrade the peptide chains starting at the ends, by cleaving off single amino acid molecules. The carboxypeptidases start at the carboxyl end, while the aminopeptidases attack the amino end. Finally, mention should be made of dipeptidases, which decompose only dipeptides. The action of proteases does not seem to be so strongly specific as that of the other



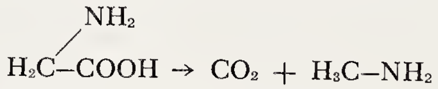
Mode of the action of proteases

enzymes, but they are adapted for the catalytic cleavage of the peptide linkage between two specific amino acids either exclusively, or at least preferentially. The end products of the proteolytic decomposition of proteins are always amino acids.

TRANSFORMATIONS AND DEGRADATION OF AMINO ACIDS

The amino acids formed in the protein breakdown process can now either be transported in the sieve elements to sites of utilization or to storage organs, or they may remain available to the cell for new syntheses. The amino acids required by the cell may not be the ones released by proteolysis, but the cell can to a certain extent synthesize the required amino acids from the proteolysis products by a process of transamination or by other reactions. The amino acids can also be further decomposed in a number of ways if they are not needed.

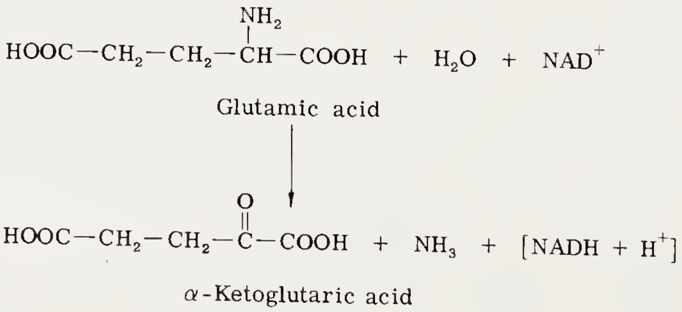
The decarboxylation of amino acids by the amino acid decarboxylases leads to the corresponding biogenic amines. Thus, for instance, the decarboxylation of glycocoll yields methylamine.



$$H_2\overset{NH_2}{C}{-}COOH \rightarrow CO_2 + H_3C{-}NH_2$$

This process occurs mostly in bacteria and in fungi; the function of the amines formed in these organisms is not clear. The amino acids lysine and ornithine can in this way give rise to the amines cadaverine and putrescine; the latter are responsible, among others, for the odor of feces. Oddly enough, both these compounds have recently also been found to occur in the ribosomes.

The oxidative deamination by amino acid oxidases yields the corresponding keto acids and ammonia; it is therefore in principle a reversal of the synthetic process described above (see p. 240). The hydrogen eliminated is taken up by the prosthetic group of the respective enzyme; this is illustrated below by a deamination of glutamic acid by NAD+ catalyzed by a specific dehydrogenase.



$$HOOC{-}CH_2{-}CH_2{-}\overset{NH_2}{\overset{|}{C}H}{-}COOH + H_2O + NAD^+$$

Glutamic acid

$$\downarrow$$

$$HOOC{-}CH_2{-}CH_2{-}\overset{O}{\overset{\|}{C}}{-}COOH + NH_3 + [NADH + H^+]$$

α-Ketoglutaric acid

The keto acids formed in protein degradation can further be decarboxylated to aldehydes, which can subsequently be oxidized to the corresponding fatty acids. The protein, carbohydrate, and fat metabolisms are therefore connected through both the above mentioned fatty acids and the keto acids; however, these connections will not be discussed in detail. It can be mentioned in this context that protein degradation along these lines for the release of energy does not normally take place in higher plants. The utilization of proteins in respiration can rather be regarded as a sign of pathological conditions, e.g., of inadequate supply of nutrients. Saprophytic microorganisms (see p. 249), on the other hand, do utilize the carbon skeleton residues of amino acids left after deamination for the release of energy.

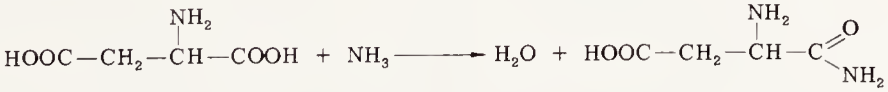
NH_3 DETOXIFICATION

The NH_3 formed in oxidative deamination is strongly toxic to the cell and its accumulation in the cell would lead to serious metabolic disturbances. The animal excretes nitrogen in the form of urea or of uric acid, but this mechanism does not operate in plants. The reason for this is that in autotrophic plants nitrogen is most frequently the limiting factor among the essential elements, and excretion of nitrogenous waste products would therefore be a luxury that plants cannot afford. They must, therefore, detoxicate the NH_3 formed, and this they can do in various ways. A few of the many possibilities will be considered below.

The simplest process, the formation of ammonium salts, is undesirable because the equilibrium of the reaction

$$NH_3 + H_2O \rightleftharpoons NH_4OH \rightleftharpoons NH_4^+ + OH^-$$

lies to far to the left. Detoxification by neutralization is therefore only possible in the presence of a large excess of organic acids. Another relatively simple process is the detoxification to acid amides, according to the equation:



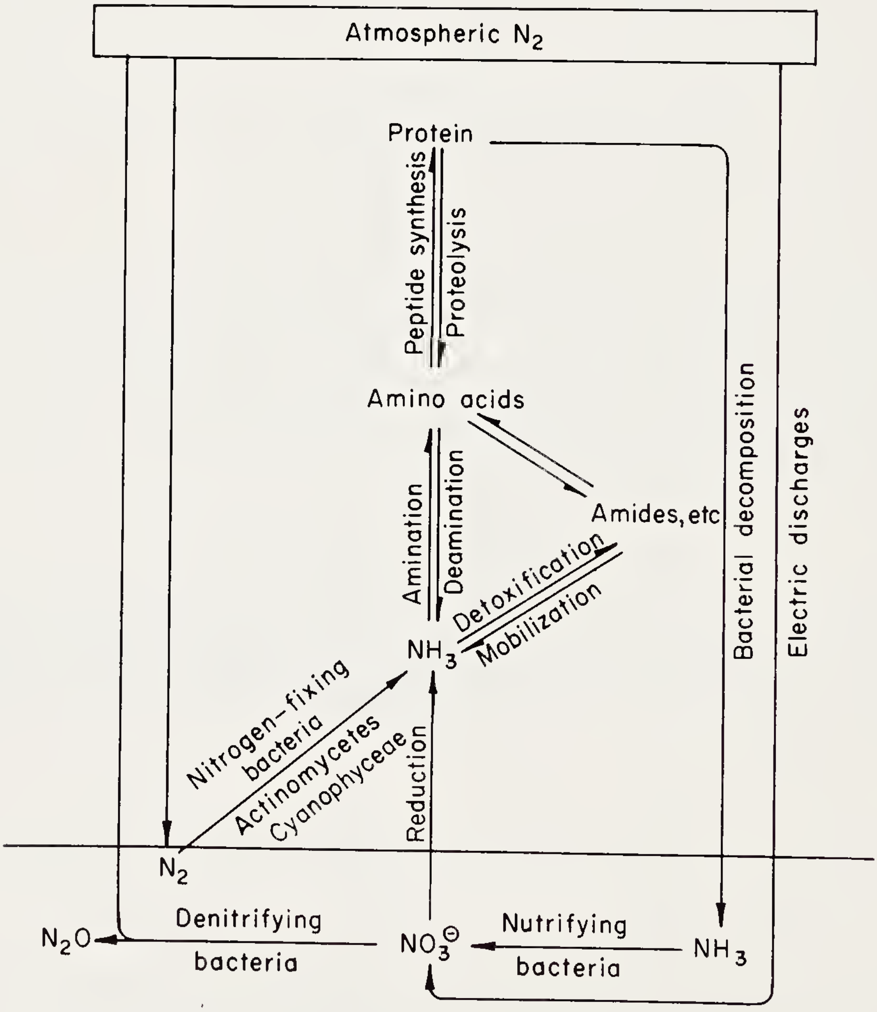
$$HOOC-CH_2-\overset{NH_2}{\overset{|}{C}H}-COOH + NH_3 \longrightarrow H_2O + HOOC-CH_2-\overset{NH_2}{\overset{|}{C}H}-C\begin{smallmatrix}\diagup O\\ \diagdown NH_2\end{smallmatrix}$$

Aspartic acid Asparagine

Other possibilities of detoxification and storage are the formation of allantoin, allantoic acid, and other compounds that can be stored as reserve nitrogen in the plant, mainly in the root. Urea is also formed in some plants (see p. 311). Nitrogen can be mobilized again relatively easily from all these compounds, to be used in further syntheses.

The Nitrogen Cycle

Similarly to carbon, which is transformed from CO_2 through photosynthesis to organic compounds and then through dissimilation back to inorganic forms, nitrogen goes through a cycle which consists of many processes. This has already been discussed in some detail; the schematic diagram below represents a summary of the nitrogen cycle.



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Chapter 13

Heterotrophy

The division of organisms into autotrophic and heterotrophic types has already been made in course of the discussion of photosynthesis (see p. 193). The heterotrophic group includes all organisms requiring ready-made organic materials as energy sources and as building materials for their tissues. This group therefore depends, directly or indirectly, on the synthetic activities of autotrophic plants. This dependence is not restricted to carbon compounds but can also include the nitrogenous materials.

The degree of heterotrophy in plants varies greatly, many organisms requiring both the carbon and the nitrogen in organic form, and others requiring only carbon but not nitrogen. Some plants rely on certain specific compounds which they cannot synthesize themselves, others can only survive in combination with another organism; yet others are autotrophic and utilize organic nutrients only in addition to their autotrophic nutrition. In many cases the type of dependence on organic materials is inadequately known. Some characteristic examples of the numerous types of heterotrophy in the plant kingdom will be discussed in the following sections.

Saprophytes

Saproprytes can be regarded as typical heterotrophic organisms. They are widely distributed in nature as putrefactive agents and are mostly members of the groups of bacteria and fungi. By secreting enzymes they transform organic materials, e.g., parts of dead animals and plants, into smaller, utilizable molecules; these molecules undergo further transformations after absorption into the cells. They often require only organic carbon compounds to be utilized mainly as sources of energy for the syntheses of their body substances. Such organisms are not very demanding and are little specialized, and they can therefore utilize a wide range of organic compounds. There is hardly any organic compound that could not act as an energy source for at least some species—even the paraffins can be decomposed. The decomposition of such very resistant compounds can, however, only be effected by certain specialized organisms.

Some saprophytes are, however, very specialized; such organisms, due to their modest selection of enzymes, can utilize only a very limited number of organic compounds. This applies especially to those organisms that also require organically bound nitrogen. Sometimes only certain quite specific compounds are utilized, which act as growth substances (see p. 323) but cannot be synthesized by the respective organisms. It is very difficult to grow such organisms (which are most frequently microorganisms) on artificial growth media.

Under natural conditions many saprophytic microorganisms are often found in association. The metabolic products of one species can then be further utilized by the other. Such association is usually described as *parabiosis*. The regular association of the autotrophic nitrite and nitrate bacteria (see p. 216) is also a case of parabiosis.

Parasites

In contrast to the saprophytes, parasites do not utilize the organic materials of dead organisms but intervene directly in the metabolism of living organisms by penetrating a host and attaching themselves to a suitable organ. The parasite's degree of dependence on the host can also vary. *Facultative parasites* can thrive equally well outside the organism, i.e., as saprophytes, while *obligate parasites* depend on the host completely. Facultative parasites among human pathogens include the pathogen of tetanus (*Clostridium tetani*) and of typhoid (*Salmonella typhosa*); obligate parasites include many Spirochaetae. The distinction between faculative and obligate parasites is, however, becoming less and less distinct among bacteria, as an increasing number of species formerly regarded as obligate parasites are being raised on artificial growth media, i.e., as saprophytes. Once they have been grown on artificial growth media they can no longer be regarded as obligate parasites, strictly speaking, since obligate parasitism is an extreme dependence on certain active substances that are normally available in sufficient quantities only in a living organism. Thus, the division of parasites into facultative and obligate groups is only of historical interest.

The parasite damage to human and animal organisms is generally not due to the utilization of nutrients by the parasite but rather to the formation of certain metabolic products (toxins) which are distinct poisons to the metabolism of the host organism (see p. 107). Apart from many pathogenic bacteria, some of which are also plant pathogens, most of the human, animal, and plant parasites are fungi.

Examples of human fungal diseases are *Tinea favosa* (ringworm) with *Trichophyton* (Achorion) *schoenleini* as pathogen, *Tinea capitus* which is caused by *Trichophyton tonsurans,* and *Moniliasis,* which is caused by *Candida* (Oidium) *albicans.* The first two of these species are Ascomycetes, while *Candida* (Oidium) *albicans* belongs to the Fungi Imperfecti (see p. 263).

There are, however, parasites among the higher plants as well, some of them partly and others wholly parasitic. Mistletoe (*Viscum album*) belongs to the former group; it is a parasite of both conifers (fir or pine mistletoe) and of deciduous trees (apples, pears, lime, etc.). The mistletoe fruit is a white berry and some birds feed on it. The seeds are then excreted with the droppings and are thus transferred to other trees where they germinate. The mistletoe first penetrates the bark of the host with cortical roots (Fig. 13.1). Contact with the host's wood vessels is established by conical haustoria which grow out of the cortical roots. Assimilation proceeds in the evergreen leaves of the mistletoe, which is therefore not truly heterotrophic. However, it is possible that it obtains from the host in addition to water and salts certain organic substances, the nature of which is as yet unknown. This could be the basis of the specialized adaptation of the various mistletoe species to certain trees.

A wholly parasitic higher plant species is clover dodder (*Cuscuta europaea*). The seedling emerging from its seed is elongated: The upper end rises above the ground and moves around in circles looking for a

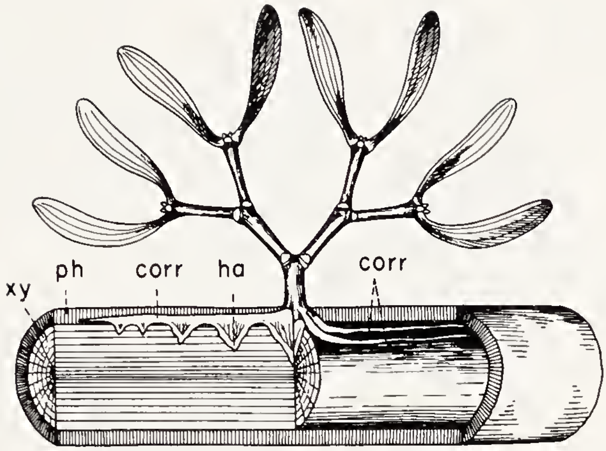

Fig. 13.1. Mistletoe (*Viscum album*) on the branch of a host: left, longitudinal section; right, perspective with the bark partly removed (magnification approx. one-half). ph, Phloem; xy, xylem; ha, haustoria; corr, cortical root. (After Goebel and Troll.)

host. If it does encounter the stem of a suitable host, it encircles it and winds up along its stem (Fig. 13.2A). With its pale shoot which contains hardly any chlorophyll, and the undeveloped scalelike leaves, the plant is not suited for autotrophic nutrition and it penetrates the tissues of the host with numerous haustoria which join with both the xylem and the phloem (Fig. 13.2B). The parasite obtains not only water and salts from the host, but also organic compounds, which often inflicts lethal damage on the host. Clover dodder is therefore a dangerous pest of many cultivated plants.

Symbiosis

Symbiosis is the temporary or permanent association of organisms belonging to different species into a close morphological union; on the whole, both partners benefit from such association. The former criterion dsitinguishes it from mere proximity, which has been described above as parabiosis, and the latter distinguishes it from parasitism. The boundary between parasitism and symbiosis is, however, not always sharp, as the benefits derived from symbiosis by the two partners are not always obvious. On the other hand, in no case does symbiosis lead to heavy damage or death of one of the partners, which is the rule in parasitism. Symbiosis occurs very often between an autotrophic and a heterotrophic partner.

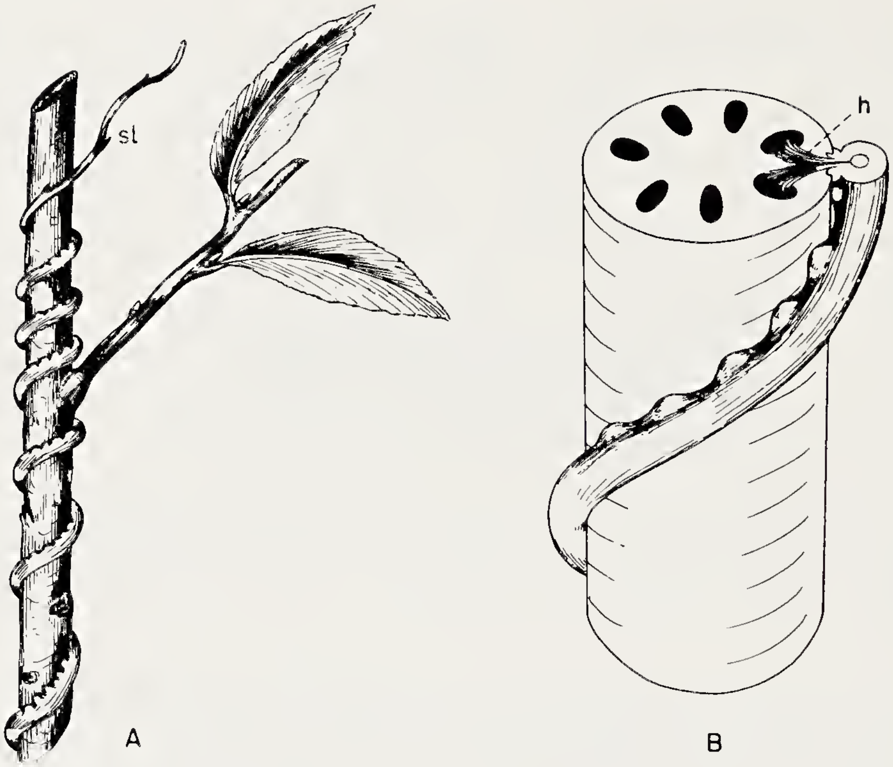

FIG. 13.2. Clover dodder (*Cuscuta europaea*). (A) Shoot winding on a willow branch (approx. to scale); (B) stem section of the parasite with haustoria penetrating the host (schematic). The cross section shows the connection between the haustoria and the vascular bundles of the host. sl, Reduced scalelike leaves; h, haustoria. (After Noll.)

ROOT TUBERCLES

One of the best known and, because of its practical importance, best studied examples of symbiosis which has already been mentioned (see p. 239) is that between the nitrogen-fixing root tubercle bacteria of the genus *Rhizobium* and leguminous plants. The bacteria, which are also found free in the soil (though they do not fix nitrogen under such conditions), penetrate the plant through the root hairs (Fig. 13.3B). They must first penetrate the cell wall, which is locally dissolved by the enzyme polygalacturonase which attacks pectin. This enzyme is produced by the host plant on contact with the bacteria. The bacteria then develop a mucilaginous tube or thread which penetrates several cortical cells, whose walls do not yet contain cellulose (cellulase is not produced); these tubes can reach the endodermis. Next, apparently stimulated by the metabolic products of the bacteria, the plant produces

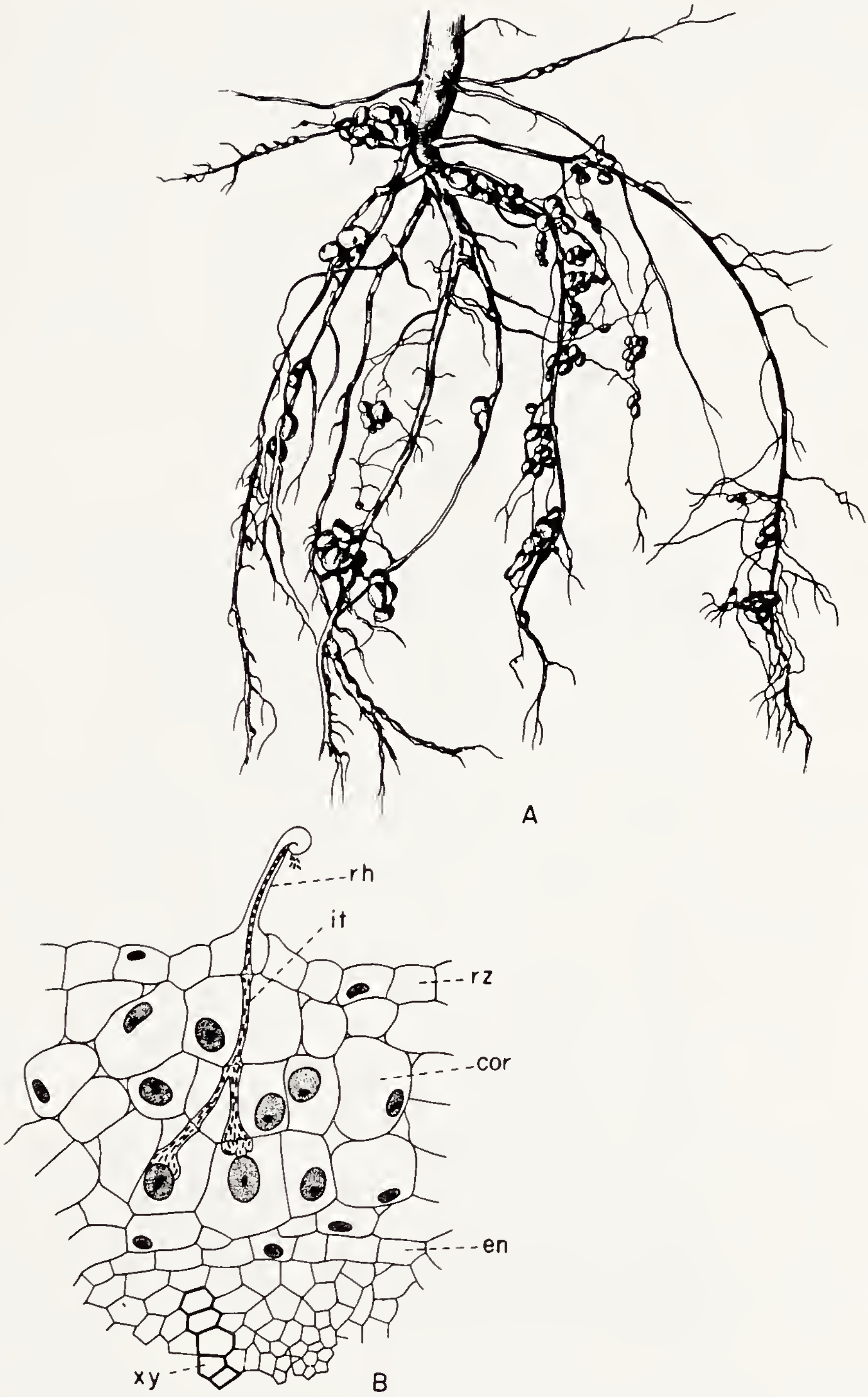

Fig. 13.3. Root tubercles: (A) tubercles on the roots of the pea (*Pisum sativum*) (approx. natural size); (B) infection of the roots of alfalfa by *Rhizobium* (schematic). en, Endodermis; it, infection tube; cor, cortical cells; rz, rhizodermis; rh, root hair; xy, xylem. [(A) After a photograph in Schaede; (B) after Thornton.]

meristems on the infected spots, from which the well-known root tubercles develop (Fig. 13.3A). The first phase of the infection is purely parasitic, while the formation of the tubercles, which corresponds to gall formation (see p. 347), can be regarded as a first defensive reaction of the infected plant limiting the infection to certain sites. The next step is a significant increase in the number of the bacteria, leading to infection of an ever increasing number of tubercle cells. Some of the bacteria now leave the infection tubes and live freely in the plasma. The fixation of elemental nitrogen occurs at this stage. More bacteria are returned to the soil after the death of the plant and disintegration of the tubercles than have infected the plant initially, and the symbiosis is beneficial to the bacteria as well.

The example of root tubercle symbiosis has been discussed above in greater detail because it shows the way in which symbiosis may have developed from parasitism. The infection by the parasite is limited by the defensive reactions of the host, which leads to the development of a dynamic equilibrium beneficial to both partners.

LICHENS

Symbiosis in lichens is of a very complete form, which has led to the development of independent taxonomic entities, although they consist of an association of an alga and a fungus. The morphological union of the two partners is so close that it gives rise to a new "organism" having a characteristic shape and constant taxonomic properties (Fig. 13.4A). A cross section of the thallus of *Parmelia* (Fig. 13.4B) shows that it contains many unicellular algae surrounded by fungus mycelia; the hyphae of the mycelia can even develop haustoria to penetrate the algal cells. In the central medullar layer the hyphae are loosely packed, while in the lower and upper sides they form relatively firm cortical layers. The algal and fungal species coupled together are specific for the respective lichen species. The algae are unicellular or thread-shaped species of the classes Chlorophyceae or Cyanophyceae, while the fungi are mainly Ascomycetes, sometimes Basidiomycetes. The fungus derives assimilates from its symbiont and supplies it with water and salts, enabling the alga to thrive in relatively dry locations. There is, however, probably more than this to symbiosis, since although the fungus and the alga can both be grown separately on artificial growth media the fungus does much better in symbiosis than on its own. On the other hand, the algae have lost their capacity for sexual reproduction. The apothecia in Fig. 13.4A are therefore the fructification organs of the lichen fungus.

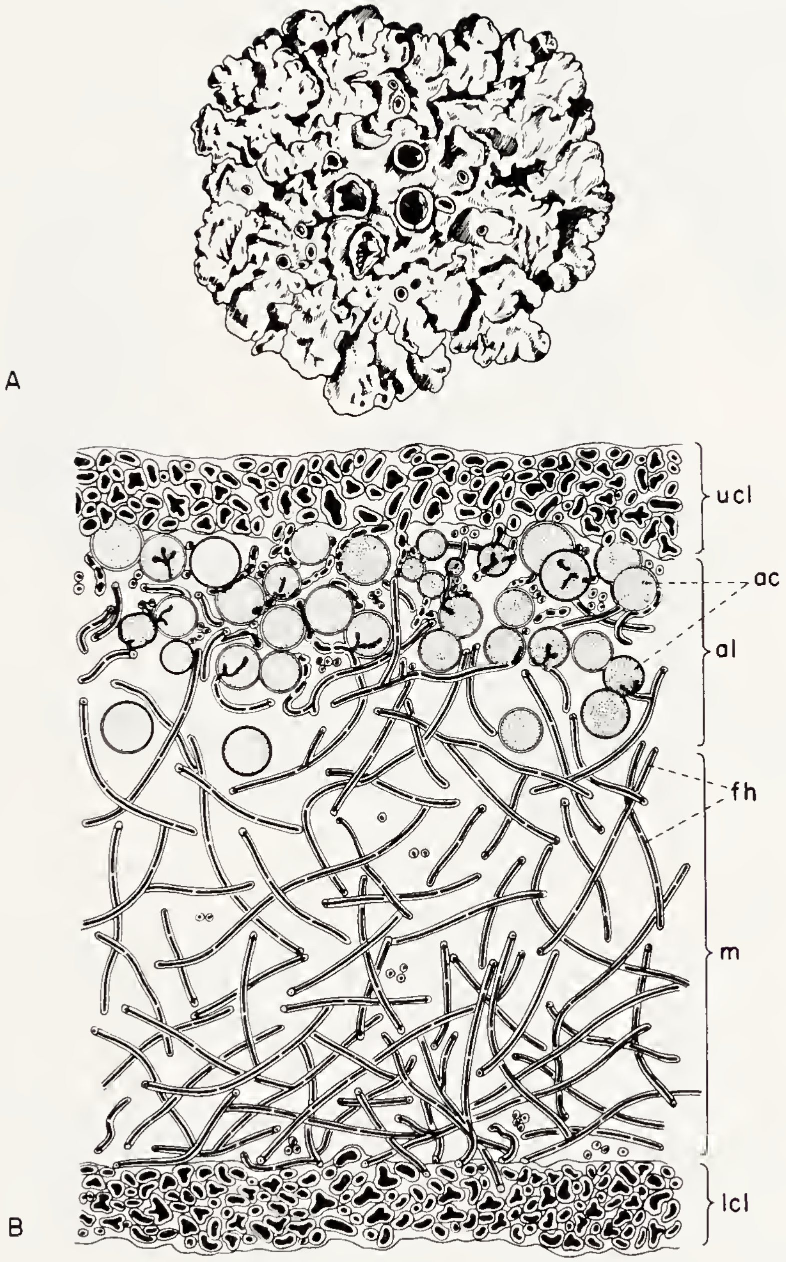

Fig. 13.4. Lichen symbiosis: (A) *Parmelia acetabulum.* Overall view (approx. to scale) with some fruiting bodies (apothecia) in the center. (B) Cross section through the thallus of the same species (approx. 250×). al, Algal layer; ac, algal cells; fh, fungus hyphae; m, medullar layer; ucl, upper cortical layer; lcl, lower cortical layer. (After Reinke and Nienburg.)

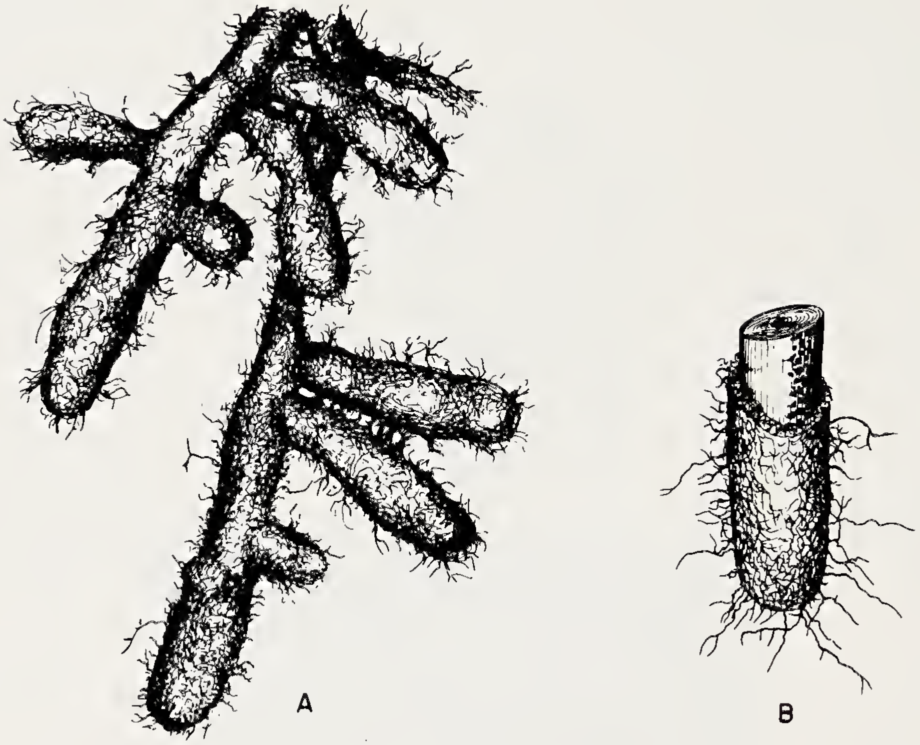

FIG. 13.5. Ectotrophic mycorrhiza. (A) Root tips of beech, swollen due to mycorrhiza infection (approx. 25×). (B) Single root with the fungus mantle partly removed (approx. 30×). [(B) After Pfeffer.]

MYCORRHIZA

This term is used to describe a symbiotic association between a fungus and a higher plant.[1] One of the more common examples is the ectotrophic mycorrhiza which occur on many forest trees of the temperate region. Here a thick mycelium surrounds the club-shaped swollen root tips (Fig. 13.5A,B). The penetration of the hyphae into the roots' cortical tissues is mainly intercellular, and the fungus obtains assimilates from the host plant, while it replaces the missing root hairs and looks after the water and ion uptake through the mycelium penetrating throughout the soil. Here, too, the association may consist of quite specific partners, e.g., *Boletus elegans* with the larch (*Larix*). Generally, however, there is no such narrow specialization; rather, both the fungi and the hosts can have several partners.

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[1] Similar symbioses of fungi with mosses and ferns lie outside the scope of this book.

In addition to the ectotrophic mycorrhiza, an endotrophic type is also known, in which the growth of the fungi is intracellular. This type is found, e.g., in orchids. The relationship between the fungus and the host is still incompletely understood, so that little can be said about the benefits derived by the two partners from the symbiosis.

There are, in any case, many transitional forms between ectotrophic and endotrophic mycorrhiza, and it is doubtful whether purely ectotrophic mycorrhizae, with exclusively intercellular growth of the hyphae exists at all. If it does not, then the distinction between ectotrophic and endotrophic mycorrhizae would become unnecessary.

Insectivores

Strictly speaking, the discussion of insectivores (= carnivores) does not belong to this chapter, as these plants can also be autotrophic under favorable conditions. The nutrients they obtain by capturing insects and other small creatures are therefore supplementary rather than essential. It is in any case difficult to define the true significance of the process. The proteins of the captured animals are decomposed in some cases by proteolytic enzymes, and the resulting amino acids are absorbed by the plant. In other cases, no proteolytic enzymes are formed. It seems, therefore, that the insectivores are mainly concerned with nitrogen. However, their mineral requirements also appear to be largely met by the insects. This is supported by the observation that insectivorous plants grow mostly on infertile soils and that their root system is often poorly developed. Three types of insectivores can be distinguished, according to the nature of their insect traps: those with adhesive traps; those with slide traps; and those with valve traps.

Drosera

This genus, represented by the sundew (*Drosera rotundifolia*), belongs to the type with adhesive traps. The leaves of this plant carry numerous tentacles which have glandular condyles at their ends and produce a sticky secretion (Fig. 13.6). When a small insect attracted by the scent comes into contact with such a leaf, it is unable to free itself. The neighboring tentacles too bend toward the center of the leaf (Fig. 13.6B), due to chemonasty or chemotropism (see p. 396), finally covering the whole insect with secretion and dissolving it completely with the exception of the chitin exoskeleton.

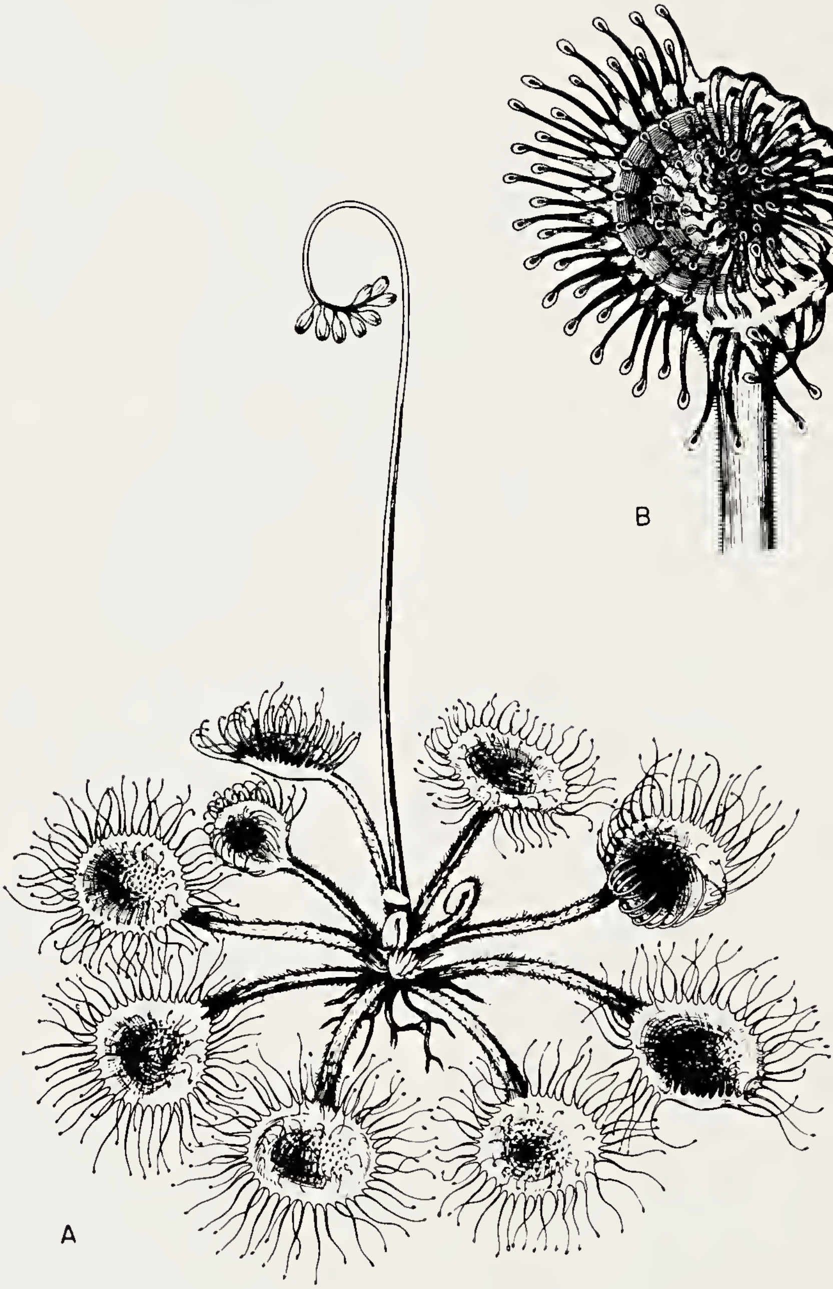

FIG. 13.6. Sundew (*Drosera rotundifolia*): (A) overall view; some leaves with tentacles bent backward (approx. 2×); (B) perspective view of a leaf (approx. 4×). The tentacles on the right-hand side are bent over a captured insect. (After Kny, Kerner, and von Marilaun.)

Dionaea

An example of the type with valve traps is the familiar Venus fly-trap (*Dionaea muscipula*) (Fig. 13.7). The two halves of the leaf are here transformed into a valve trap and the petiole is flattened and widened. The two half leaves can be made to close by shaking (seismonasty, see p. 397), by touching the tactile bristles, and by chemical stimulation p. 395). The closing movement is relatively fast and is caused by changes in the turgor pressure in the mesophyll cells positioned obliquely to the center rib. Growth processes are also involved. The bristles at the trap edges close trellislike and make it impossible for the insect to escape. The numerous glands at the upper leaf surface then

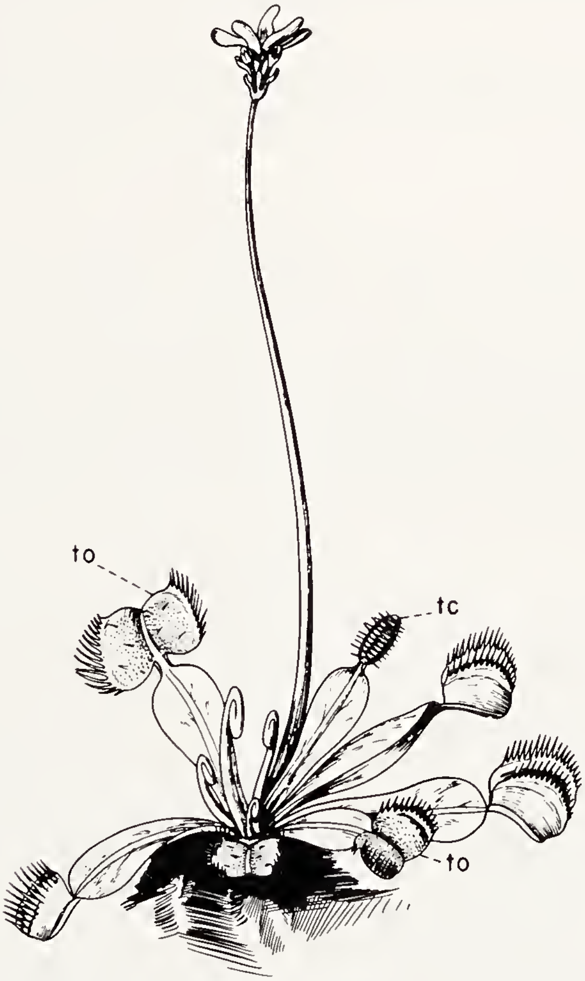

Fig. 13.7. Venus fly-trap (*Dionaea muscipula*), overall view (magnification approx. one-half). tc, Closed trap; to, open trap. [After Kny (1879).]

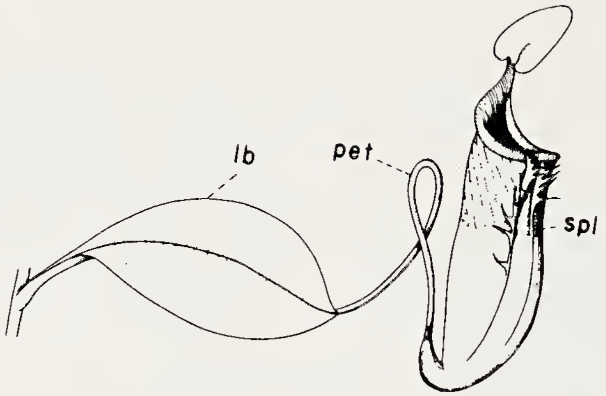

FIG. 13.8. *Nepenthes fusma;* pitcher-shaped leaf (approx. one-third normal size). lb, Leaf base; spl, specialized leaf blade modified into cup; pet, petiole. (After Troll.)

produce a secretion which dissolves the captured animal until only the chitin remains.

Nepenthes

The tropical pitcher plants (*Nepenthes*) capture insects by making use of the slide trap principle. The pitcher-shaped leaves (Fig. 13.8) have smooth edges and walls. If an insect, attracted by gland secretions, arrives at the edge of the pitcher, it falls into the watery fluid in the pitcher; it is questionable whether or not the pitchers secrete proteolytic enzymes. The role of the leaf blade is taken over by the flattened leaf base.

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Chapter 14

Reproduction

The discussion so far has been restricted to the structure and activities of plant organs engaged in acquisition and conversion of energy and in the synthesis and translocation of materials. These organs are said to be vegetative, while organs serving for the purposes of reproduction and propagation are called reproductive.

The terms reproduction and propagation are often used interchangeably, although their meaning is by no means identical. The purpose of reproduction is essentially fulfilled when an organism produces a daughter organism before its death, and thus ensures survival of the species. The concept of propagation, on the other hand, involves an increase in the numbers of the population. In nature, reproduction is actually also propagation in the majority of cases, as many daughter organisms perish before they can propagate themselves. Survival of the species could not, therefore, be ensured by the production of a single daughter organism.

While in unicellular organisms each cell is capable of reproduction, increasing cell sophistication, organization, and concomitant differentiation lead to the development of special reproductive cells or organs in which the reproductive units are produced. A distinction must be made between asexual (vegetative) and sexual reproduction.

Vegetative Reproduction

Vegetative reproductive units are the results of mitotic divisions. In the simplest case vegetative propagation consists of a division of the organism into parts that continue to grow separately. Since one organism gives rise to at least two in this way, the process can be regarded as propagation. In unicellular organisms the process is one of cell division. In many cases, however, the multicellular parts of thread or tissue thalli of algae or fungi can also continue growing as independent entities. Even severed organs or parts of organs of many higher plants have the ability of regenerating the missing organs; this is utilized in the practice of propagation by cuttings.

Apart from the division of the unicellular organisms, the examples given above are mainly the results of violent, external, mechanical influences and are therefore of accidental character. However, many plants develop special organs which enable them to reproduce vegetatively in a spontaneous manner independent of such accidents. The main examples of this are the brood bodies and the spores.

A special case is that of the already mentioned globules of *Volvox* (see p. 112); these develop daughter globules by curving inward (Fig. 5.8A). After the lapse of some time the daughters detach themselves from the mother globule, but they can only be set free after the mother has died. This is a case intermediate between propagation by simple cell division, as in unicellular organisms, and the development of multicellular brood bodies found, e.g., on many mosses (*Marchantia*) (Fig. 5.17A).

BROOD ORGANS

These frequently develop on side shoots or in place of axillary shoots. Examples of this kind have already been described as in strawberries. The stolons of strawberries develop buds at regular intervals, which grow into plants with their own root system (Fig. 6.17E). In *Bryophyllum* there are remainders of meristem tissues on crenate leaves; these form into daughter plantlets while still on the mother leaf (Fig. 14.1), eventually fall to the ground and develop into independent plants. Other reproductive organs, which have already been mentioned, are the bulbs (Fig. 7.13), stem tubers (Fig. 6.17G), and root tubers; these mostly give rise to more than one plant and are therefore also the means of propagation.

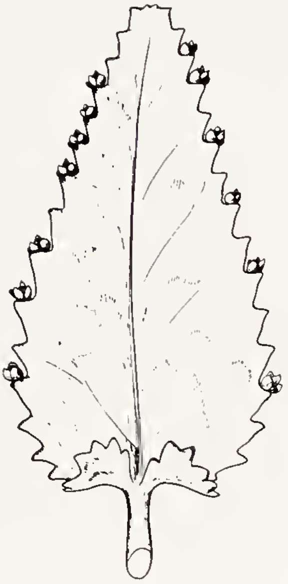

Fig. 14.1. Development of plantlets from residual meristems in the leaf notches of *Bryophyllum daigremontianum*.

Spores

Spores are unicellular reproductive units, which often also serve as resting stages for the survival of unfavorable vegetative periods. In the latter case they are enclosed in solid, resistant walls. They are widely distributed throughout the plant kingdom and in many cases represent the sole means of reproduction, as in many fungi (Fungi Imperfecti), no sexual forms of which are as yet known. The spores develop in large numbers, mostly on or in special carriers. Various types of spores can be distinguished according to their shape and mode of formation, i.e., essentially according to external morphological features.

Zoospores are the reproductive units of many algae and of some lower fungi. They always have flagellae and are similar in appearance to the flagellates (Fig. 5.5). The sessile types of zoospores anchor themselves after a certain time and grow into new thalli. The containers in which the zoospores are formed are called sporangia, specifically zoosporangia. In unicellular organisms the whole cell functions as a zoosporangium; its content is divided on zoospore formation and the empty cell then dies off. In many filamentous algae, too, simple vegetative cells may become zoosporangia. In other instances the sporangia differ in shape from the vegetative cells. In many algae, e.g., in *Chlorella vulgaris* (Fig. 5.6), non-motile spores occur as well; these are known as aplanospores.

The zoospores (swimming spores) occur exclusively in aquatic forms or on types adapted to very moist locations; the aerial spores borne by animals or the wind, on the other hand, occur on organisms suited to terrestrial life in relatively dry locations.

Arthrospores are resting (permanent) cells which develop as links of a cell thread. In its widest sense the term embraces the cells of bacteria which do not form spores (see below) and which can survive unfavorable conditions for long periods by allowing the plasma and the cell wall to thicken. In true spores, however, the protoplast quits the spore on germination and leaves the empty shell behind. Many Cyanophyceae also develop special resting cells, which act as links in a cell filament and are usually larger than the vegetative cells. The protoplasts of the arthrospores divide only on germination; vegetative reproduction is therefore not accompanied here by propagation.

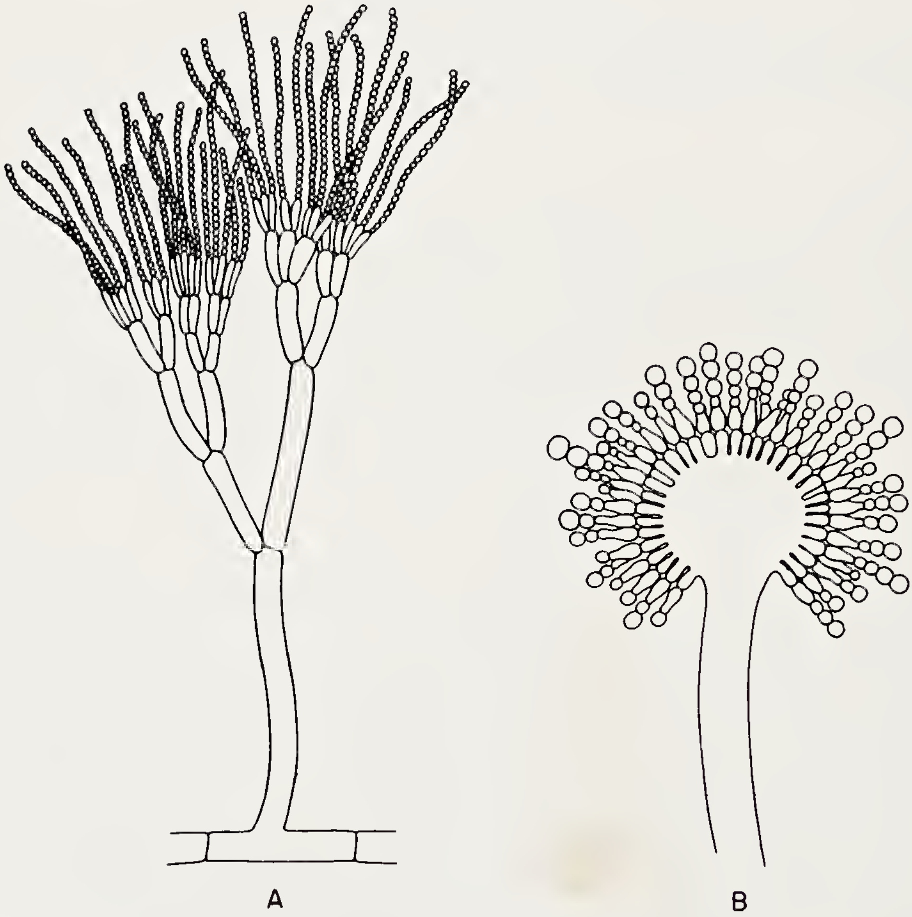

FIG. 14.2. Formation of conidiospores: (A) *Penicillium notatum;* (B) *Aspergillus niger.*

Exospores, which are also known as conidiospores, develop by tying off hyphal tips as special sporangium carriers which are often of characteristic shape. Two well known fungi can serve as examples, *Penicillium* (Fig. 14.2A) and *Aspergillus* (Fig. 14.2B). In some cases the conidia are polynuclear and homologous with a whole sporangium.

Endospores, on the other hand, always develop in special containers, the sporangia, from which they are released on destruction of the sporangium wall. An example of this is furnished by *Mucor* (Figs. 5.9 and 14.3). The spores of the *Bacillus* and *Clostridium* bacteria develop inside vegetative cells (Fig. 5.1G), and are, therefore, usually described as endospores. They are released on the decomposition of the cell wall and can remain in suspended animation over long periods. On falling into a favorable environment, the spores germinate after swelling and opening up of the spore wall (Fig. 5.2), and only then do they multiply by division. This, therefore, is also a case of vegetative reproduction without propagation.

Basidiospores (see p. 285) also belong to the exospores by definition, while the ascospores (see p. 284) and spores of mosses and ferns (see pp. 275, 278) belong to the endospores. All these spores are, however, formed in the course of a sexual reproductive cycle or alternation of generations, and are usually the direct products of meiosis. They cannot, therefore, be regarded as "asexual" and equated with the types of spores discussed above. It would be preferable not to use the term "spore" for one of the two groups, but as it is firmly established it would be desirable to acknowledge the special character of the spores formed in the alternation of generations by describing them as "*meiospores*," spores resulting from *meiosis*.

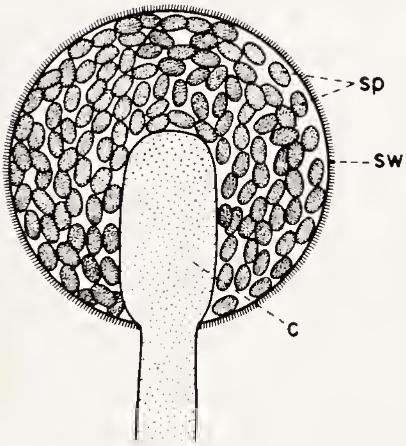

FIG. 14.3. Formation of endospores in *Mucor mucedo*. c, Columella; sp, spores; sw, sporangium wall. (After Brefeld.)

Sexual Reproduction

Sexual reproduction is characterized by: (1) the union (fertilization) of two haploid, 1*n* sexually different cells (gametes) to form a diploid (2*n*) zygote; and (2) the formation of (1*n*) gametes in animals or (1*n*) meiospores in plants at some point of the development cycle by *meiosis*. More precisely, fertilization is usually characterized by the union of sexually different nuclei. It is true that in most cases the union of the nuclei (karyogamy) follows directly the union of the plasmas (plasmogamy); however, in some organisms (such as fungi, see p. 283), the processes of plasmo- and karyogamy are separated both in space and in time by a phase in which the cells have two nuclei (dikaryophase).

MEIOSIS

The zygote produced by the union of two haploid gametes is diploid (2*n*) as it contains both a paternal and a maternal chromosome complement. The process of zygote formation would lead to further doubling of chromosome complements in every generation, unless the numbers of chromosomes were previously halved (i.e., to a set of 1*n*) during the formation of gametes. This actually happens during meiosis which consists of two coupled division processes.

However, the reduction in the number of chromosomes is only one of the objects of meiosis. Another aim that is no less important is mixing of the parental genetic material by means of the random distribution of paternal and maternal chromosomes and also fresh recombination of the genes located in the chromosomes by fertilization and by chromosomal aberrations such as inversions, translocations, and exchanges of segments (see below). Consequently, the course of meiosis differs considerably from that of mitosis, in which the cleaved halves of all chromosomes are passed on from cell to cell (see p. 61). This becomes apparent already before meiosis, when the nuclei increase their size above the normal level, but it is especially obvious in the meiotic prophase, whose course is much more complicated and which also lasts much longer than in mitosis. In contrast to mitosis, the chromosomes in this case are not directly transformed from the elongated active into the compact transport form, but the parallel conjugation or *pairing of the homologous chromosomes* (same chromosome bearing same genes but one from each parent) occurs already during the gradual helical winding process of the chromosome filaments. This leads to the formation of very characteristic images to which special names have been given.

In the leptotene stage the thin elongated chromosome filments still occur as tangled coils (Fig. 14.4A); they can, however, be stained to give better contrast due to their progressive enrichment with nucleic acids. They are in a somewhat more ordered state in the zygotene, with the threads shortened and wound into helices and the homologous chromosomes appearing in pairs (Fig. 14.4B); this pairing process is completed in the pachytene stage (Fig. 14.4C). In this condition all the mor-

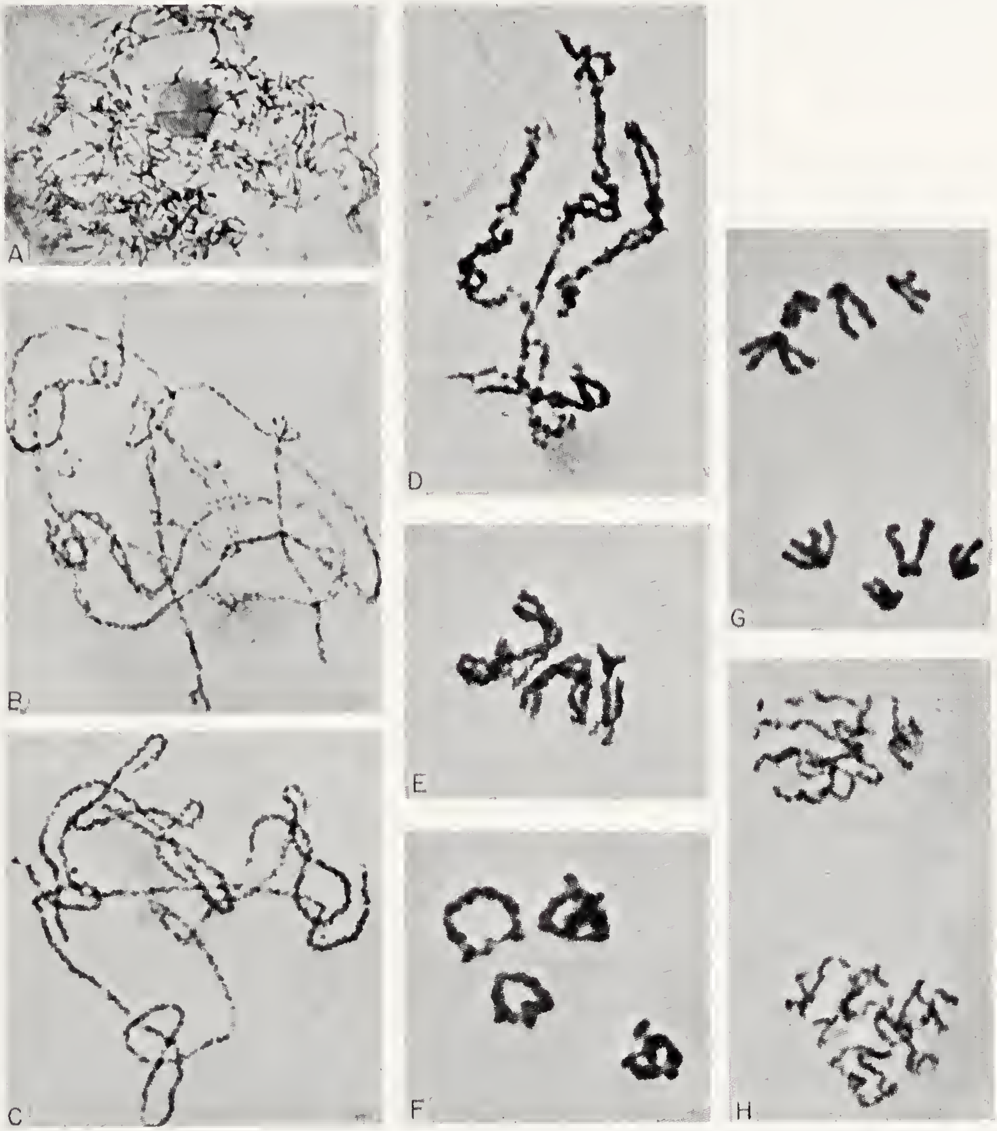

Fig. 14.4. Stages of meiosis from the anthers of *Bellevalia romana* (*Hyacinthus romanus*). (A) Leptotene; (B) zygotene; (C) pachytene; (D) early and (E) late diplotene; (F) diakinesis; (G) first telophase; (H) daughter nuclei. [From Oehlkers (1956).]

phologically distinguishable and corresponding parts of homologous chromosomes are accurately paired. Next, in the diplotene stage (Fig. 14.4D) the longitudinal duplication becomes apparent in each homologous chromosome (Fig. 3.10D), and by late diplotene (Fig. 14.4E) they are described as the four chromatids of a tetrad (Fig. 14.5D). The paired chromosomes are also described as bivalents. *Only the centromeres remain undivided at first.* Separation of the homologous chromosomes begins in the diplotene (Fig. 14.4D,E) with continued shortening of the threads; the daughter chromatids remain together. The separation does not, how-

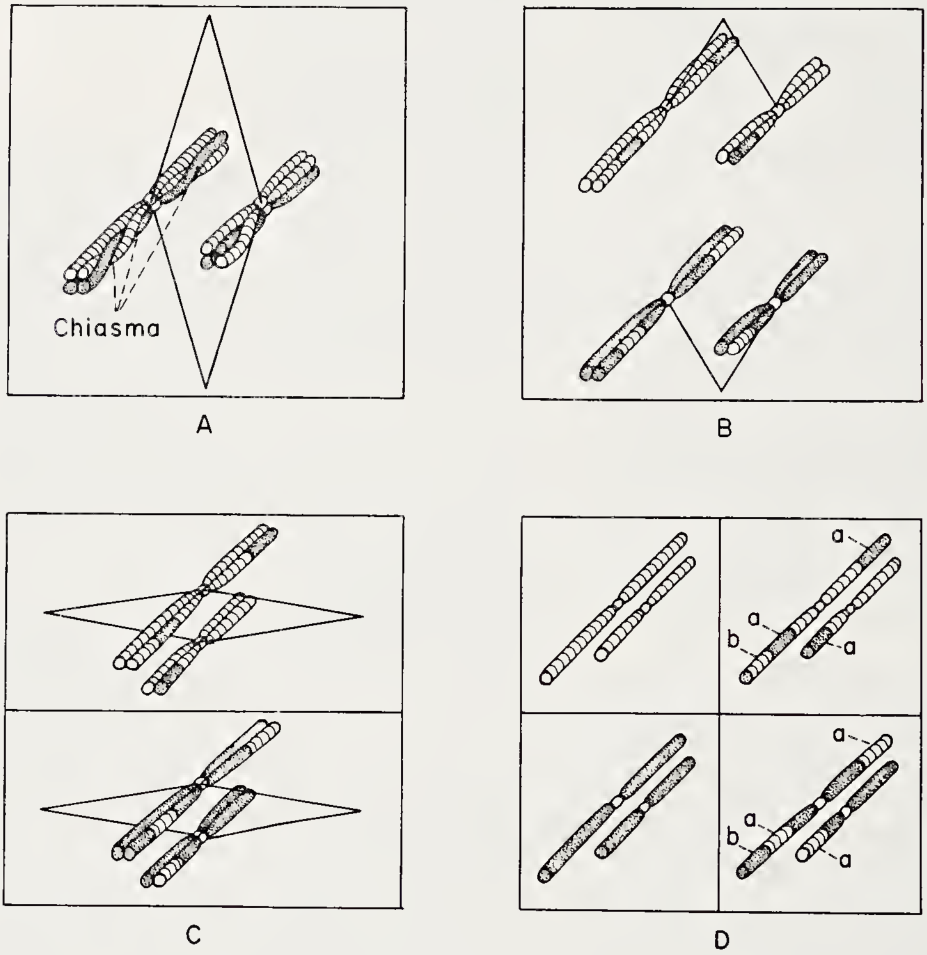

FIG. 14.5. Schematic illustration of meiosis in a cell with two sets of homologous chromosomes. The homologous chromosomes are marked differently. (A) and (B), first division; (C) and (D), second division stages of meiosis. (D) shows the final separation of the chromosomes (tetrad) into chromatids. The unmarked chromosome segments are prereduced, like the centromeres; those marked (a) are postreduced as a consequence of segment exchange, while those marked (b) are prereduced as a consequence of reversed exchange.

ever, go to completion; the chromatids remain in positions in which they cross over (chiasma formation), remaining coupled for some time (Fig. 14.5A).

The chiasmata are usually but not always the visible manifestations of *crossing over.* This last term describes the exchange of chromatid segments which occurs by cleavage of the chromatids followed by attachment of the cleavage products to the (sister) chromatid lying opposite (Fig. 14.5B). This exchange of segments is in fact an exchange of genetic material between the chromatids of paternal and maternal origin (Fig. 15.5). In this way new combinations arise inside the chromosomes, which can be identified in genetic experiments (see p. 292).

In diakinesis (Fig. 14.4F) the shortening of the chromosomes is completed. The tetrads move next to the nuclear membrane, which is dissolving. A spindle apparatus develops, and the tetrads are ordered in an arrangement corresponding to the equatorial plane of the cell. The paired chromosomes are completely separated in the anaphase and move to the poles at telophase with their centromeres pointing toward the poles (Fig. 14.4G). Which of the two homologous chromosomes moves to which particular pole is apparently left to chance; thus, normally both paternal and maternal chromosomes are found at each pole. There is, therefore, a rearrangement of the genomes.

The nuclei formed in the telophase in meiosis differ significantly from the telophase in mitosis. The chromosome helixes lengthen only slightly (Fig. 14.4H), and the cells do not reconstitute a nuclear membrane. After this intermediate phase, known as interkinesis, the second stage of meiosis commences; this proceeds like mitosis. The cleaved half chromosomes (daughter chromatids) separate from each other, since the centromere is now divided, so that the two stages of meiosis give rise to four haploid nuclei. Meiosis and cytokinesis result in four cells, meiospores in plants, spermatids in male animals, or one large modified oogonial cell and 3 polar bodies in female animals (Fig. 14.5D). On development of the cell "walls," each of these cells contains one chromatid from the chromatid tetrad formed during the pairing and duplication of homologues. Since, as has already been mentioned, the centromere remains undivided during the first stage of meiosis, it is the homologous chromosomes (daughter chromatids) in this phase that are being separated and not sister chromatids of homologous chromosomes. This is, therefore, essentially a mode of division traditionally described as prereduction or a reductional division. The second division is referred to as a postreduction or equational (mitotic) division. Due to the segment exchange, however, the chromatids often consist partly of paternal and partly of maternal sections. Sections which stayed with their original centromere from the start, or which have returned to it (Fig. 14.5), follow the prereduction type of division, while the exchanged sections undergo the postreduction type provided that the corresponding sister chromatid section has remained in its original position. Because of crossing over (segmental interchange) there is little point in retaining this terminology; the noncommittal terms "first" and "second" meiotic divisions are to be preferred.

FORMATION OF GAMETES

As has already been explained, meiosis is an essential condition for the development of gametes. It does not follow, however, that it can only occur during the formation of gametes; it can in fact occur much earlier, e.g., during the germination of the zygote, the first divisions of the zygote nucleus. The difference between the two types is obvious. In the first case the organism proper is diploid (i.e., a diplont), and the haploid phase is restricted exclusively to the gametes (Fig. 14.6A). In the second case, the organism is a haplont and the diploid phase is restricted to the zygote (Fig. 14.6B). Both types are known to occur. For example, among the algae already mentioned, *Ulothrix* and *Spirogyra* in the Chlorophyceae are haplonts, while the Diatoms and *Acetabularia* in the Chlorophyceae are diplonts.

The gametes are formed in the gametangia. In unicellular and other simpler organisms the gametangia are normal vegetative cells whose contents are subdivided during gamete formation, while the gametangia of higher plants are multicellular containers of specific shapes. However, differentiation with increasing degree of organization affects not only the gametangia but also the gametes; this manifests itself in the increased size and loss of mobility of the female gamete. In fungi the development

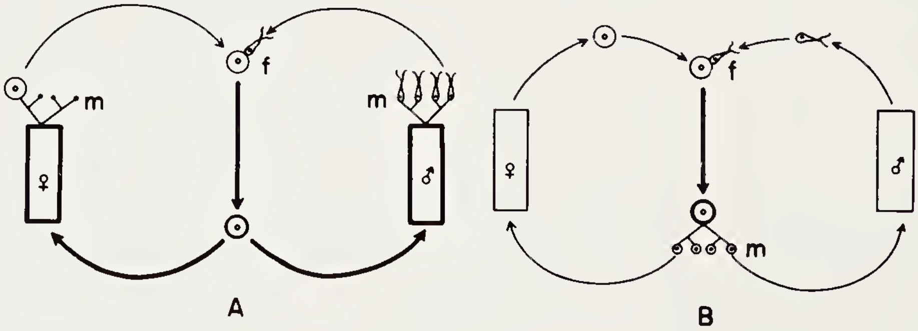

FIG. 14.6. Schematic diagram of the development process of a diplont (A) and haplont (B). Sexual forms are chosen in both cases. The haplophase is shown by thin and the diplophase by thick lines. f, Fertilization; m, meiosis.

leads to suppression of gamete formation, and finally even to disappearance of the gametangia. The following individual forms of sexual reproduction can be distinguished.

Isogamy (Fig. 14.7A)

The differently sexed gametes are of the same external shape, and cannot therefore be distinguished as male (♂) and female (♀), but can only be described as + and − according to their mating behavior (physiological anisogamy).

Anisogamy (Fig. 14.7B)

The male and female gametes are of similar shape, but the female macrogametes are larger than the male microgametes.

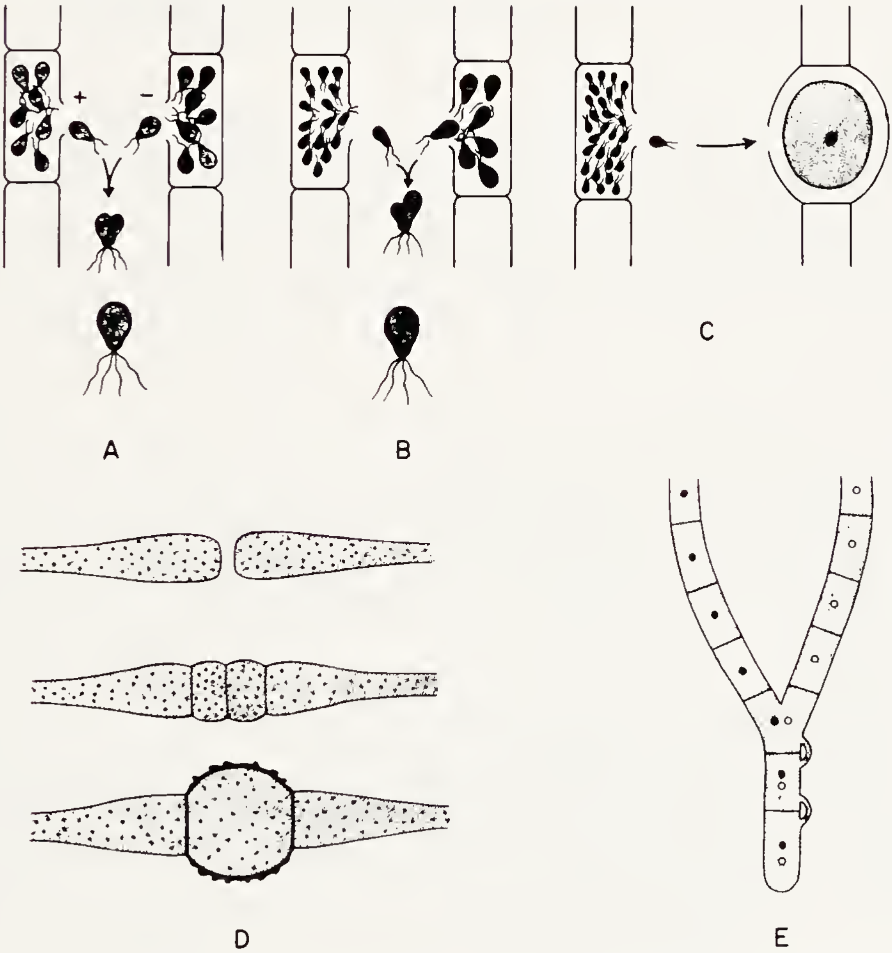

Fig. 14.7. Schematic diagram of various forms of sexual reproduction. (A) Isogamy; (B) anisogamy; (C) oogamy; (D) isogamous gametangiogamy; (E) somatogamy. (Further explanations in text.)

Oogamy (Fig. 14.7C)

The female gametes, which are described here as ova, have no flagellae, are static, and often remain enclosed in the gametangium. They are usually much larger than the male gametes, the spermatozoids. The gametangia also differ in shape, and therefore they have been specially named. The female ones are known as oogonia and the male ones as spermagonia. The ova are stationary, and so the spermatozoids must find them and, if necessary, even penetrate the oogonium. While the oogonium consists of one cell, in which one or more egg cells are produced, the flask-shaped ovum receptacles of the higher mosses and ferns (see below) have a special wall divided into cells, i.e., they are multicellular. They are therefore known as archegonia to distinguish them from the oogonia. The same holds for the male gametangia: The multicellular ones are known as antheridia to distinguish them from the spermagonia.

Gametangiogamy (Fig. 14.7D)

This term describes a special case of sexual reproduction in which gametes probably do not develop at all; rather the polynuclear gametangia fuse or at least join together. Here, too, isogamous gametangiogamy can be distinguished from the anisogamous type; in the former, the gametangia are externally similar (*Mucor,* Fig. 14.7D), while in the latter the gametangia are differently shaped (Ascomycetes, see p. 284).

Somatogamy (Fig. 14.7E)

The most extreme case of reduction occurs in somatogamy, which is characteristic of the Basidiomycetes (see p. 285). Here not even the gametangia develop any more; body cells unite instead. These cells are of similar external shape but differ in their mating behavior. Plasmogamy and karyogamy are separated in time and space by the dikaryophases (see p. 266).

Several types can also be distinguished with respect to the mating behavior and to the distribution of sexual organs. In the dioecious[1] (sexual) species there are two morphologically different groups of individuals. One of these produces only female, the other only male sexual cells and organs; or, in isogamous forms, + or — cells and organs. Self-fertilization is therefore impossible here. In monoecious species both male and female sexual cells are formed in the same individual, and self-fertilization is possible here in principle providing it is not prevented by sexual incompatibility. Such autosterile organisms therefore require a partner for sexual reproduction in spite of their monoecious nature. Where no sexual organs are formed, as in the Basidiomycetes, the sexes can no longer be distinguished. In these cases the possibility of mating is determined exclusively by the sexual compatibility or incompatibility, and the participants can only be distinguished by their mating behavior. Sexual incompatibility is determined genetically (see p. 316). In many cases the sexual cells may develop into a new organism even without fertilization, i.e., without the formation of zygotes (parthenogenesis).

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[1] The terminology of the separate and mixed sexual state is somewhat confused. In the following discussion only the terms "monoecious" and "dioecious" will be used, irrespective of whether they refer to the haplo or to the diplo phase. This simplification seems justified in view of the introductory character of the present discussion.

The Alternation of Generations

Sexual reproduction is necessarily bound up with a regular alternation in the phases of the nuclei. One of the two nuclear phases extends only over a very limited time in the reproductive cycle. In haplonts the diploid phase is restricted to the zygote, while in diplonts the haploid phase extends only over the gametes (Fig. 14.6). In both cases, however, the reproductive cycle is completed in one generation in those organisms which live for longer periods of time.

The term "alternation of generations" refers to a regular alternation of two or more generations (G_1, G_2, etc.) which reproduce in different ways. In the majority of cases only two generations are involved; in plants one of these, the gametophyte generation, reproduces by gametes, and the other, the sporophyte generation, by meiospores (see p. 266). In addition, both generations are often capable of vegetative reproduction.

The alternation of generations in plants is often connected with an alternation in the phases of nuclei (K_1, K_2). In this so-called heterophasic (antithetic) alternation of generations, the zygote gives rise to the diploid sporophyte. The latter in turn gives rise by meiosis to meiospores; on germination, these develop into haploid gametophytes. While the antithetic alternation of generations can be regarded as the most frequent type, the alternation of generations and that of nuclear phases are two basically independent processes which need not necessarily be coupled together. This becomes apparent, as in the red algae (Rhodophyceae), where the alternation takes three generations to complete; two of these must necessarily have the same nuclear phase, i.e., must be homophasic. There are, however, other types of Rhodophyceae, in which the cycle of development is completed in only two homophasic generations, e.g., the genus

Batrachospermum. Here the diploid phase is restricted to the zygote. In animals, both phases of the alternation of generations (e.g., medusa and polyp in Anthozoa) are diploid.

Finally, the alternation of generations can be connected with a change in shape (M_1, M_2). In this case it is described as heteromorphic. The variation in shape has in many cases led to the two generations being regarded at first as independent plants and given different names. However, the alternation in shape is no more essential to the alternation of generations than is the alternation of nuclear phases. Many cases are in fact known in which both generations look alike (isomorphic alternation of generations, e.g., *Ulva*).

ISOMORPHIC ALTERNATION OF GENERATIONS IN *Cladophora* (Fig. 14.8)

Cladophora (Chlorophyceae), whose external appearance has already been discussed (see p. 116), has gametophytes that are externally alike but are differentiated into + and − forms. The + and − isogametes develop in any one of the thread-shaped cells which are transformed into gametangia by subdivision of their contents and emit a large number of gametes having two flagellae each. Two of these unite to give rise to a zygote, and this germinates to form a diploid sporophyte which does not differ exter-

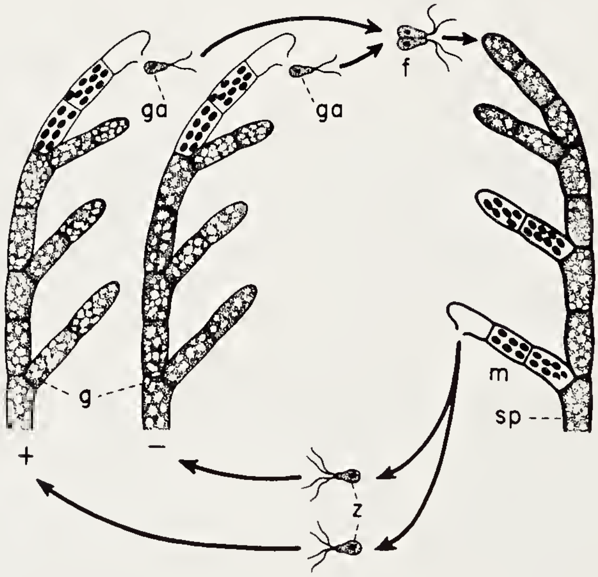

FIG. 14.8. Isomorphic, heterophasic alternation of generations in *Cladophora* (schematic). The haploid phase is drawn with thin and the diploid phase with thick outlines. g, Gametophyte; ga, gametes with two flagellae; f, fertilization; m, meiosis; sp, sporophyte; z, zoospores with four flagellae.

nally from the gametophytes. The sporangia on these are also simple, unmodified, filamentous cells; in these sporangia, meiosis gives rise to meiozoospores. These are differentiated into 50% of + and 50% of − forms and develop into haploid gametophytes which are either + or −. *Cladophora* therefore exhibits a heterophasic, isomorphic alternation of generations that can be described by the following symbols: $G_1K_1M_1$–$G_2K_2M_1$.

ALTERNATION OF GENERATIONS IN THE ARCHEGONIATES

An example of a heteromorphic, heterophasic alternation of generations is exhibited by the objects of Wilhelm Hofmeister's classic studies, the archegoniates. This concept covers the mosses and the ferns, which have very similar female sex organs (archegonia) irrespective of the great variety in their external morphology.

Mosses (Fig. 14.9)

For the sake of simplicity, Fig. 14.9 represents only the alternation of generations in a monoecious moss. If the haploid meiospores of a moss find themselves in a favorable environment, they germinate to form the protonema: The latter is a multiply-branched filament, each thread consisting of a single row of cells. The protonema develops multicellular buds as sideshoots which then develop into (gametophyte) moss plants (see p. 123) with stems and leaflets. The gametophyte therefore undergoes an alternation of shape; it is dimorphic. There is, however, no alternation of generations or of nuclear phases associated with this alternation of shape, which again demonstrates the independence of the alternations of generations of shape and of nuclear phases. The moss plant then develops archegonia and antheridia; these occur on different plants in dioecious species. On ripening, fertilization occurs when the chemotactically (see p. 396) attracted spermatozoids penetrate the collar of the archegonium. One of these spermatozoids unites with the ovum to form a zygote. This germinates, without leaving the archegonium, into the diploid sporophyte which remains anchored in the moss plant at its base. The sporophyte does not become a completely independent individual, but it is capable of photosynthesis and is not heterotrophic. In the spore capsule the tissues separate into the sterile capsule tissue and the archespore; the meiospores arise from the cells of the latter by meiosis. In the mosses the opening formed after the shedding of the operculum is closed by a serrated edge, the peristome; the serrations are arranged radially

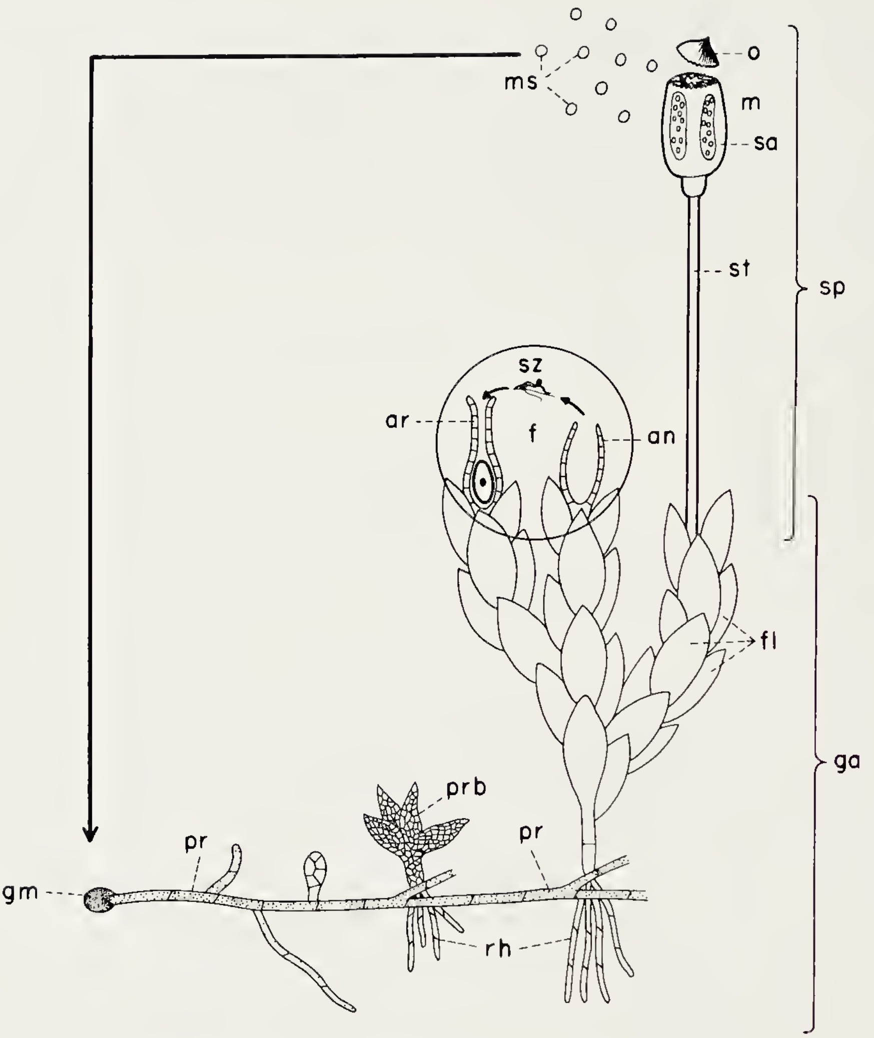

FIG. 14.9. Heteromorphic, heterophasic alternation of generations of a monoecious leafy moss (schematic). The encircled sex organs are strongly magnified. an, Antheridium; ar, archegonium; fl, foliage leaf; o, operculum; ga, gametophyte; f, fertilization; sa, spore capsule; prb, protonemal bud; gm, germinating meiospore; m, meiosis; ms, meiospore; pr, protonema; rh, rhizoid; st, stalk; sp, sporophyte; sz, spermatozoid.

toward the center. These serrations are able to execute hygroscopic movements, bending inward or outward depending on the relative humidity and thus opening or closing the entry. In this way the spores are dispersed gradually and only under favorable weather conditions.

Pteridophytes (Fig. 14.10)

In principle, the alternation of generations in ferns and other pteridophytes is very similar to that in the mosses. However the one significant

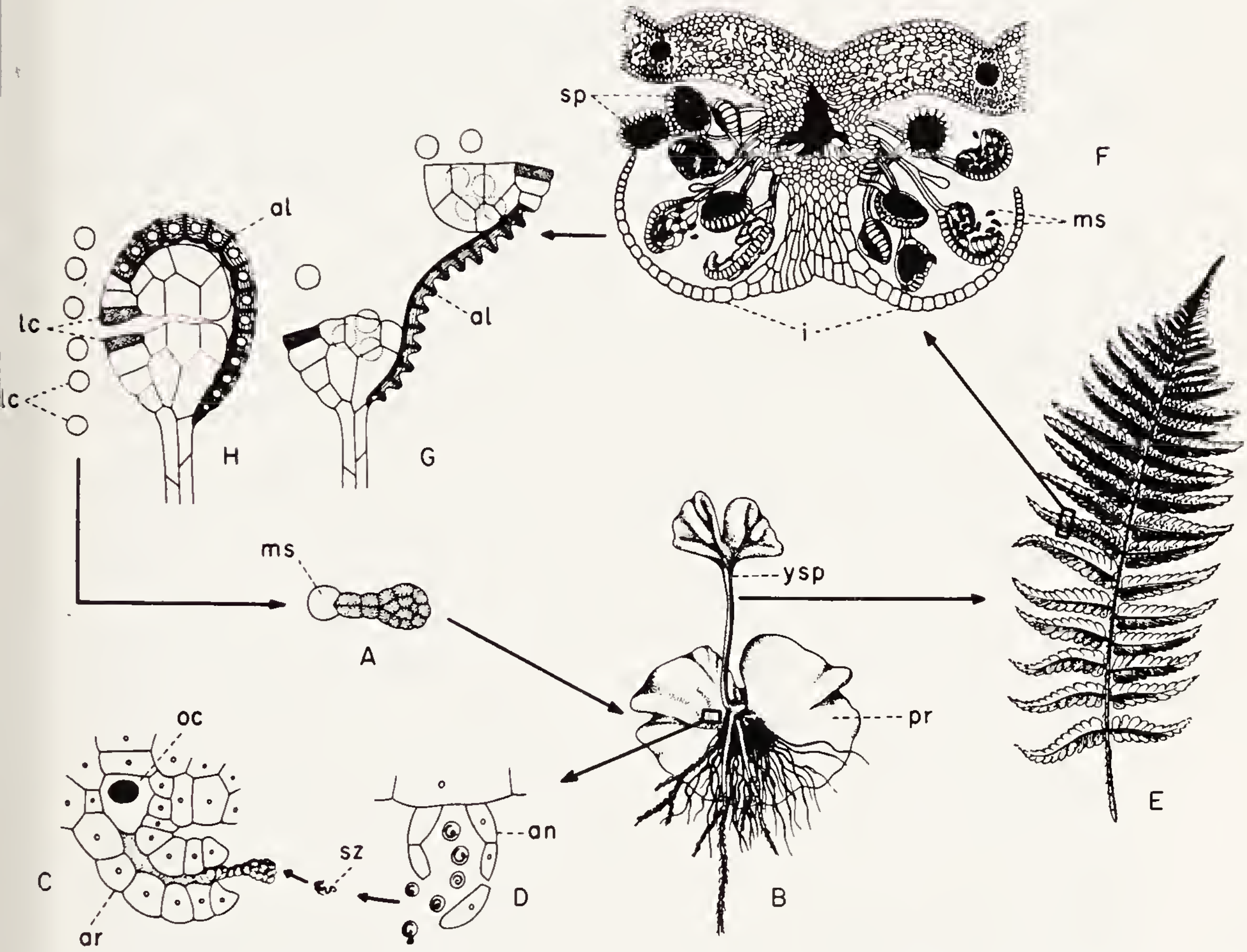

FIG. 14.10. Heteromorphic, heterophasic alternation of generations in an isosporous fern (*Dryopteris felixmas*, shield fern) (partly schematic). (A) Germinating meiospore; (B) prothallium giving rise to a young sporophyte; (C) archegonium; (D) antheridium; (E) sporophyte leaf covered with sori; (F) cross section through a sorus; (G) sporangium opened by the tangential stress of water films in the annulus cells; (H) half sporangia, after the breaking of the outer wall, returned to their original position while the meiospores are being ejected. al, Annulus; an, antheridium; ar, archegonium; oc, ovum cell; i, indusium; ysp, young sporophyte; pr, prothallium; sp, sporangium; ms, meiospores; lc, lip cells; sz, spermatozoids. (After Sinnot-Wilson, Kny, and Stocker.)

difference is that here the permanent plant is the sporophyte, while the gametophyte [the prothallium (Fig. 14.10B)] is a small thallous organism of limited life-span which develops directly from the germinating meiospore. In the isosporous ferns, which are generally monoecious, the antheridia and archegonia develop on the same prothallium (Fig. 14.10C, D). After fertilization, which proceeds in the same way as in mosses, the zygote gives rise to the diploid sporophyte; this finally develops into a self-contained fern plant. The sporangia grow on leaves, the so-called sporophylls. In many cases, as also in *Dryopteris*, the sporophylls do not differ externally from the sterile foliage leaves. The sporangia occur here in groups (sori) on the reverse side of the leaves and are covered with a veil, the indusium (Fig. 14.10E,F). However, in many genera the shape of the sporophylls differs from that of the foliage leaves. In either case the spore mother cells develop from the central tissue of the sporangia, the archesporial cells, by numerous cell divisions, and these in turn give rise to meiospores by meiosis. The spores are released after the breaking open of the sporangium which is operated by a special mechanism, the annulus (see p. 371), and are distributed by the wind (Fig. 14.10G,H).

Thus, in the isosporous pteridophytes, the size relationship between gametophytes and sporophytes is heavily displaced in favor of the latter, as compared with the mosses. This reduction of the gametophytes goes even further in the heterosporous pteridophytes. In the latter, the meiospores are differentiated into micro- and megaspores formed on micro- and megasporophylls, respectively. The micro- and megaprothallia developing after germination consist of only a few cells, and no longer leave the meiospores on germination but immediately start to develop the antheridia and archegonia. As has already been recognized by Hofmeister, a line of development extends from the mosses through the isoporous to the heterosporous pteridophytes; this development is expressed in the alternation of generations in the increasing reduction of the gametophyte, on the one hand, and in the increasingly higher development of the sporophyte on the other. The development reaches a climax in the spermatophytes.

Reproduction of the Spermatophytes

The alternation of generations in the spermatophytes can only be verified after a closer investigation of the conditions of reproduction of this group. The reduction of the gametophyte here has progressed so far that it forms a small part of the highly developed sporophyte and is externally no longer visible at all.

In the spermatophytes the micro- and megasporophylls, here known as stamens and carpels, occur together in sporophyll whorls located at the ends of the floral axis and are described as flowers. Similar micro- and megasporophylls already occur on some heterosporous pteridophytes

(Selaginella); they are therefore not characteristic of Spermatophytes alone.

In many cases the sporophylls of the Spermatophytes are surrounded by the perianth, a shell of sterile leaves; these leaves are of different shapes and often brightly colored. The perianth is mostly divided into the calyx (sepals) and corolla (petals). When the members of both the calyx and the corolla are similar, the perianth is known as a perigonium. Flowers without perianths are also known to occur.

Apart from complete flowers, in which the stamens and the carpels are present together, there are some flowers which have either the stamens or the carpels alone. The former are known as staminate and the latter as pistillate flowers. Flowers of both kinds can occur on one and the same individual, as on hazel, or they may be restricted to different individuals as on the yew and the willow. On ash, both staminate and pistillate flowers occur alongside complete ones on the same individual.

The stamens (Fig. 14.11A) can be divided into the filament and the another. The latter consists of two interconnected thecae, each of which contains two pollen sacs. Each pollen sac is homologous to a microsporangium in the heterosporous ferns. The haploid microspores develop from the archesporal tissue by meiosis. The microspore nucleus divides once to produce a two-celled microgametophyte containing one vegetative and one reproductive cell. At the same time a nutritive layer in the anther, the tapetum, adds a thick spore coat and the entity is known as a pollen grain, which is usually shed in this two-celled condition. The stamens as a whole are known as the androecium.

The carpels (megasporophylls), which are described collectively as the gynoecium,[2] carry the ovules or megasporangia, which lie free on the surface in the gymnosperms; in the angiosperms, on the other hand, the carpels are always joined into one or several ovaries; the ovules are found inside. The ovary (Fig. 14.11A) narrows upward into a thin style, the top of which can be split into stigma branches as in the present example. The sum total of the ovaries, style, and stigma is described as the pistil.

The ovules, which occur singly or severally in the ovaries of the various species, are produced by a special tissue of the carpels, the so-called placenta; they remain connected to it by means of the funiculus. Beginning at the base of the ovule, the chalazal end, one (gymnosperms) or two (angiosperms) integuments are formed and grow up over the inner tissue complex, the nucellus, and leave a gap open at the end opposite to the chalaza; this gap is the micropyle. The carpels are homologous with the megasporophylls, and the nucellus is homologous with the megaspor-

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[2] The often used term "gynaeceum" is etymologically incorrect.

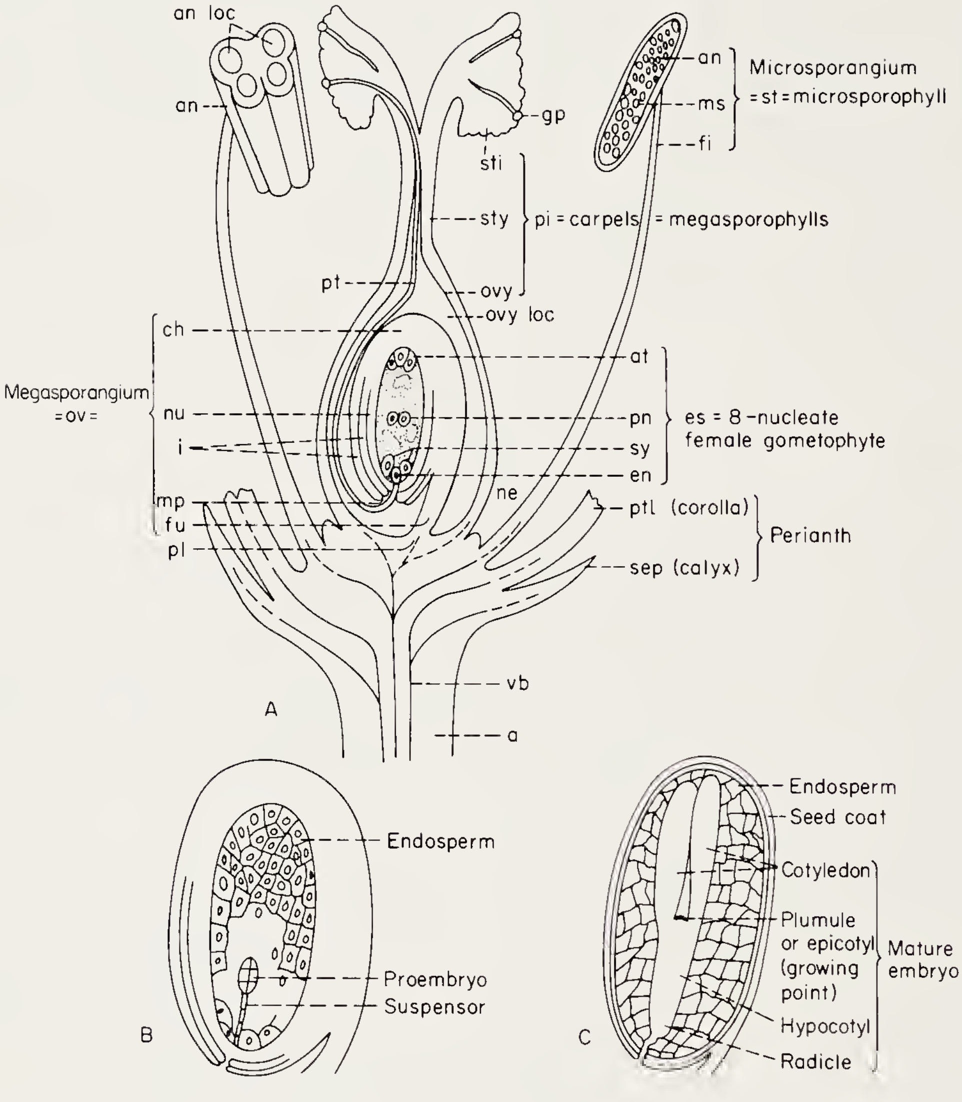

FIG. 14.11. (A) Schematic structure of a flower. a, Floral axis; vb, vascular bundle; Perianth—sep, sepal; ptl, petal; Microsporangium=microsporophyll=st, stamens—an, anther; an loc, anther locules; ms, microspores; fi, filament; Microgametophyte—gp, germinating pollen grain; pt, pollen tube; Megasporophylls=carpels=pi, pistil—sti, stigma; sty, style; ovy, ovary; Megasporangium=ov, ovule; pl, placenta=attachment of ovule to ovary; fu, funiculus=stalk connecting ovule to placenta; mp, micropyle; i, integuments; nu, nucellus; ch, chalazal end of ovule; Female gametophyte=es, embryo sac—at, antipodals; pn, polar nuclei; sy, synergids; en, egg nucleus. (After Sachs.) (B) Section of ovule showing formation of endosperm and development of the proembryo. (C) Section of mature or ripened ovule, the seed.

angium of heterosporous ferns. In the nucellus one cell, the megaspore mother cell, undergoes meiosis. Although plants exhibit several patterns of ovule development, usually three out of the four cells formed die off, while the fourth, corresponding to the functional megaspore, gives rise to the female gametophyte. This occurs in the following way: The embryo sac increases in size and the nucleus divides first into two nuclei; these move to opposite ends of the embryo sac, where each of them divides twice more, so that eight nuclei are produced in all. On the pole facing the micropyle, the egg nucleus and two other cells, the synergids, separate from the embryo sac as the so-called egg apparatus; the three antipodal nuclei collect at the opposite pole (Fig. 14.11A). The two remaining nuclei then move toward each other and fuse to form the polar nucleus. The ovule is now ready to be fertilized.

There is no doubt that the ripe embryo sac corresponds to a germinating megaspore, i.e., to a megaprothallium or female gametophyte. This can be seen in the gymnosperms, in which the oospheres are enclosed in nearly complete archegonia which lie in the embryo sac. In the angiosperms this too is reduced. It is tempting to regard the synergids as the residues of archegonia.

The reduction of the male gametophytes proceeds even further. As soon as the pollen grains reach the stigma, they germinate with the development of pollen tubes. These penetrate the tissues of the stigma and the style and reach down to the micropyle. The reproductive cell undergoes another division, and both the resulting nuclei migrate through the pollen tube into the embryo sac (Fig. 14.11A). As they are surrounded by a thin plasma layer, they are described more accurately as sperm cells. The germinating pollen grain therefore corresponds to the microprothallium or microgametophyte. This extreme case of reduction is also connected with the heterosporous ferns through the gymnosperms, in which one can still discern residues of the antheridium. Both the male and female gametophyte are reduced to a few cell residues in the angiosperms.

As soon as the pollen tube reaches the embryo sac, the two sperm cells are transferred to the embryo sac, mostly to one of the two synergids. This behavior is described as siphonogamy. While one sperm cell fuses with the egg nucleus to form a zygote, the second sperm cell moves to the polar nucleus and fuses with it to yield a triploid endosperm nucleus. This and the plasma of the embryo sac then give rise to the (also triploid) endosperm (nutritive tissue) by free nuclear division; the cell walls form later (Fig. 14.11B). The activity of the two sperm nuclei is known as double fertilization.

The fertilized egg, which surrounds itself with a cellulose wall, gives rise by periclinal divisions to a series of 4–6 cells. The proembryo then develops by multiple division out of only the front cells of the series; the remaining cells develop into a so-called suspensor, which elongate to push the embryo deeper into the nutritive tissue and also supplies it with nutrients. The embryo is at first an approximately globular organism (spherical stage, Fig. 14.11B); it gives rise next in the heart stage by differentiation to a radicle at the pole facing the micropyle, while the cotyledons develop at the opposite pole. In dicotyledons the growing point (plumule or epicotyl) lies between the two cotyledons placed on either side; in monocotyledons it is found on one side of the single cotyledon.

SEED

During the development of the embryo and the endosperm, the integuments develop into the testa or seed coat. The product consisting of the seed coat, the endosperm, and the mature embryo is known as a *seed* or ripened ovule (Fig. 14.11C), the characteristic distributive unit of the spermatophytes. The embryo resumes its growth only on germination of the seed, at first at the expense of the nutritive tissue, and grows into a new sporophyte. In many cases, however, no special nutrient tissues are formed and the storage of reserve materials occurs in the cotyledons.

FRUIT

Development of the seed proceeds simultaneously with transformation of the carpels (ovary wall) and possibly other flower parts into *fruits*. When seeds and fruits are ripe, the seed distribution proceeds in various ways, depending on the special type to which the fruit belongs. The dehiscent fruits (capsules, pods) open up and scatter the seeds. In the achenes (nuts, drupes, berries) the seed remains enclosed in the fruit, and the two are distributed together. If the seed then falls into a favorable environment, the radicle emerges from the micropyle and anchors the seed to the ground. The cotyledons may either remain below the surface (hypogeous germination) or may emerge above the ground by the lengthening of the hypocotyl, after having pried the seed coat open (epigeous germination, Fig. 7.4). They then also become green. The stem axis has a bud at the top. This is the epicotyl or plumule; its first leaves, the primary leaves, develop rapidly.

The Reproduction of Fungi

The sexual reproduction of fungi exhibits an extraordinary variety of types, ranging from the simplest forms of isogamy through anisogamy and oogamy to full reduction of the gametes and finally even to suppression of the development of gametangia. Only a few characteristic examples can be considered here.

PHYCOMYCETES (Water Molds)

The highest developed forms of this group are the Zygomycetales, a group mostly characterized by isogamous gametangiogamy. When the mycelia of two parents meet, the hyphae branches grow upon each other and swell to form club-shaped gametangia with many nuclei; these fuse directly without the formation of gametes to form a coenozygote[3] (Fig. 14.7D). The nuclei of the two parents actually fuse only somewhat later. Plasmogamy and karyogamy are therefore separated in this case in time if not in space. The coenozygote then surrounds itself with a rigid wall and develops into a zygospore. Meiosis occurs at once on germination of the zygospores. The Zygomycetales are therefore haplonts.

ASCOMYCETES

This group is typically monoecious and partly autosterile (see p. 273). The case illustrated here (Fig. 14.12) is one of autosterility. Nuclei of one and the same mycelium are potentially of either sex. The male sex organ is known as the androecium, the female one as the ascogonium. On the top of the latter is formed a papilliform growth, the trichogyne, which grows on to the androecium and fuses with it (plasmogamy). This is therefore a case of gametangiogamy. The nuclei move out of the androecium into the ascogonium where they fuse with the nuclei of the latter. This is followed by the emergence of ascogenous hyphae from the ascogonium, in which the two nuclei always undergo simultaneous, i.e., conjugated, division; thus each cell contains two nuclei (dikaryophase). Finally, the aduncate (hooked) cell develops, in which both nuclei divide once more. Out of the four nuclei two of opposite sexes remain in the aduncate cell,

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[3] It would be wrong to describe the coenozygote simply as a zygote. In contrast to the zygote, which is the product of the union of two mononuclear gametes, the coenozygote arises by the fusion of two polynuclear gametangia.

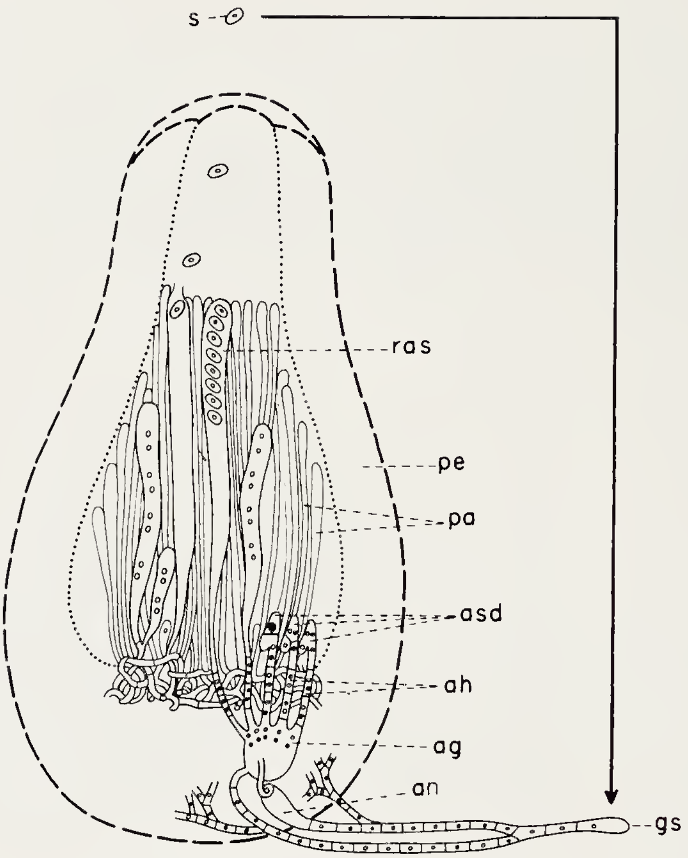

FIG. 14.12. Developmental cycle of a monoecious Ascomycete (schematic). ras, Ripe ascus; an, andrangium; asd, ascus development (zygote nucleus shaded); ag, ascogonium; ah, ascogenous hyphae; gs, germinating spores; pa, paraphyses; pe, perithecium; s, ascospores.

while the third migrates into the stalk cell and the fourth into the lower part of the aduncate cell. After the separation of the upper part of the aduncate cell by cell walls, the two nuclei fuse to form the zygote nucleus (karyogamy). The hooked end of the aduncate cell then fuses with the stalk cell and the nucleus moves back into it; this may be followed by renewed hook formation. The aduncate cell now develops into an ascus; meiosis and a further mitotic division give rise to eight haploid ascospores which are ejected and germinate to yield another mycelium. The diploid phase is therefore restricted to the zygote. There are many variations of the basic process outlined here.

The asci together with sterile hyphae, the paraphyses, form the hymenium; this develops either inside a fruit body or on the surface of one. The former are known as perithecia and the latter as apothecia.

BASIDIOMYCETES (Fig. 14.13)

Since the Basidiomycetes develop no sex organs, the occurrence of a sexual act between two mycelia depends exclusively on their sexual compatibility or incompatibility (cf. p. 273). The mycelia, which develop from germinating basidiospores, can grow vegetatively for long periods. When the mycelia of two parents meet, their cells fuse (plasmogamy) without the formation of gametangia (somatogamy). This gives rise to a dikaryotic mycelium, which has characteristic clamps (clamp mycelium). The two nuclei undergo conjugated division every time the cell divides. On the apical cell there develops a hook which then bends backward. One of the nuclei migrates into this hook, while another nucleus (which differs from the first) remains in the lower part of the cell. The other two

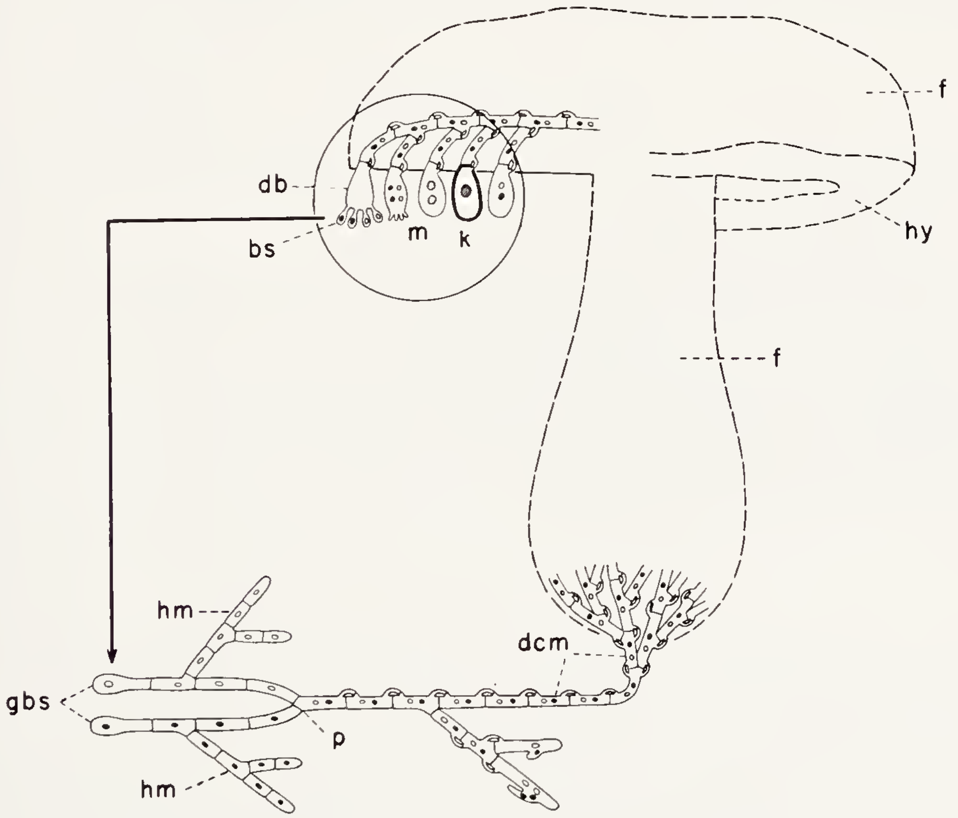

FIG. 14.13. Developmental cycle of a *Basidiomycete* (schematic). The fructification organs (encircled) and the hyphae are magnified more strongly than the fruit body. The nuclei of the two parents are shown in black and in white. db, Development of basidium; f, fruit body; hm, haploid mycelium; hy, hymenium; k, karyogamy; gbs, germinating basidiospores; m, meiosis; p, plasmogamy; dcm, dikaryotic clamp mycelium; bs, basidiospores.

nuclei move into the apical region and the cell separates itself from the base by the development of a transverse wall. Now the hook fuses with the cell below and emits its nucleus into it; the latter then becomes dikaryotic as well. The clamp separates itself from the apical cell by the development of a wall.

Finally the clamp mycelium grows into a fruit body whose shape varies from case to case; this again gives rise to a hymenium. Here the ends of the clamp mycelium swell into a basidium, in which the fusion of nuclei (karyogamy) takes place. Four nuclei are formed by meiosis. Short excrescences, the sterigmata, appear at the tips of basidia; one nucleus migrates into the swollen ends of each of these. The sterigmata then tie off as basidiospores and are scattered. Two out of four of the mycelia developing from the germinating basidiospores possess the same sexual incompatibility factor. They therefore cannot mate with each other but can easily do so with any one of the other two mycelia.

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Chapter 15

Heredity

The resemblance between the external appearance (phenotype) of the parents and of the offspring produced in reproduction is substantial. The members of a given species or other taxonomic unit are also more or less like each other (see p. 400). The underlying reason for this similarity or identity is the basic problem of the study of heredity (genetics).

The first experiments in genetics were carried out in the last century by Gregor Mendel. The rules derived from these experiments, now known as Mendel's laws of heredity, were published by him in 1866 but remained unnoticed until they were rediscovered in 1900 by Correns, Tschermark, and de Vries. The development of genetics since that date has been very rapid. Originally animals and higher plants were used as the experimental material; more recently bacteria and viruses have also been utilized. With the aid of studies on viruses and bacteriophages it has recently become possible to clarify the molecular basis of genetic processes, so that our present views on the essence of genetic processes rank among the highest achievements of the human spirit, even though many of our ideas are still hypothetical.

Needless to say, in an introductory work like the present book, the results and problems presented can only be a selection from a large quantity of material and a selection that is unavoidably subjective. For further details the reader should consult textbooks on genetics.

The Analysis of the Genotype

The *phenotype*, the physical appearance of an organism, results from a large number of characteristics which are partly morphological and partly physiological. It must be remembered that morphological characteristics are themselves the results of physiological processes. The realization of a particular phenotype is governed by genes which possess continuity, i.e., are typically passed on unaltered from one generation to the next. The sum total of these genes is known as the *genotype*. However, the genes do not determine a characteristic property directly, but only the reactions of an organism during its development to certain external factors, i.e., its reaction norm. The number of such reactions during ontogenesis, i.e., the lifespan of an organism, is very large, and they can be conducted in various ways by changes in the external conditions; it is therefore reasonable to expect that organisms belonging to the same genotype could differ in their final appearance. Such acquired and uninheritable variations in external appearance are known as modifications (see p. 351).

LOCATION OF GENES

Both genetic experiments and cytological studies have shown that the genes, which follow Mendel's laws in the process of inheritance (see below), are located in the chromosomes. The sum total of genes in a chromosome complement is known as the *genome;* this term does not cover the extrachromosomal genetic factors, which shall be discussed later (see p. 317).

It has already been mentioned (see p. 270)that organisms can be classified into haplonts and diplonts. In the haplonts, the phenotype reflects the genes of only one chromosome complement, while in the diplonts the genes of both genomes are involved. The genes corresponding to each other are located at sites exactly corresponding to each other in the homologous chromosomes.

A gene can occur in two or more different states known as *alleles*. When the alleles of a gene pair are identical, the organism is said to be homozygous; if they are different, it is heterozygous for this gene pair. The alleles are given either large or small letters, i.e., *A* and *a*, *B* and *b*. A diploid organism can therefore be *AA*, *aa*, or *Aa*. The first two are *homozygous*, and the last is *heterozygous*.

It is obvious that these descriptions can only apply to diploid organisms; a haplont, in which only the zygote is a diplont can always contain only one of the two allelic genes, and can itself therefore never be heterozygous (cf. Fig. 15.17).

MENDEL'S LAWS

Considering the phenotype of an individual, one cannot as a rule identify a particular characteristic with the particular gene giving rise to it. It is only possible to do this by "labeling" a certain gene, by following its effect on the development of the phenotype. This is done by means of crossing (hybridization) experiments.

In the simplest case, two homozygous strains are used for this purpose, differing in one or more allelic pairs. The allelic pairs of one parent are called *AA*, *BB*, etc., while the corresponding pairs of the other parent are *aa*, *bb*, etc. All gametes of the former can therefore contain only the alleles *A*, *B*, etc. while the gametes of the latter can contain only the alleles *a*, *b*, etc. The daughter organisms resulting from the crossing (first filial or F_1 generation) are hybrids, *Aa*, *Bb*, etc. Mono-, di-, and polyhybrids are distinguished according to the number of allelic pairs in which the parents (parental or P_1 generation) differ. They contain the gene pairs *Aa*, *Bb*, etc., and are therefore heterozygous with respect to these pairs. The hybrids of the F_1 generation may further be crossed with each other; the mode of the distribution of pairs of characteristics in the F_2 and successive generations can then be used for inferring the genetic nature of the respective genes.

Rule of Uniformity or Unity in Genes and Characters

Mendel found that the plant behaved in inheritance as though it were composed of independent distinct characteristics or traits which could exist in any combination with others. Those characteristics or traits conditioned by a single pair of alleles are said to be *unit characters*, independent in inheritance.

Dominance

When two strains which differ only with respect to one allelic pair (*AA* or *aa*) are crossed (single-factor crossing) the hybrids of the F_1 generation are uniform. When the hereditary process is of the intermediate type,

P_1 AA × a a
P_1 gametes Ⓐ Ⓐ ⓐ ⓐ
F_1 Aa

		♂	
		A	A
♀	a	Aa	Aa
	a	Aa	Aa

they are intermediate between their parents with respect to the development of their characteristic. In our example, the chosen characteristic is the color of the flower of *Mirabilis jalapa,* i.e., red and white, and the intermediate is therefore pink (Fig. 15.1). *When the inheritance process is of the dominant type* (e.g., *AA* = red), however, *all the hybrids are similar to the parent with the dominant allelic pair* (e.g., *Aa* = red), while the recessive allele (*a* = white) does not become apparent at all. Thus, all hybrids of *Urtica pilulifera* and *Urtica dodartii* have dentate leaves (Fig. 15.2) as the "straight-margined" allele is recessive. Which of the paternal and maternal organism belonged to which genotype is here irrelevant, the reciprocal hybrids are alike (principle of reciprocity; for exceptions see p. 317).

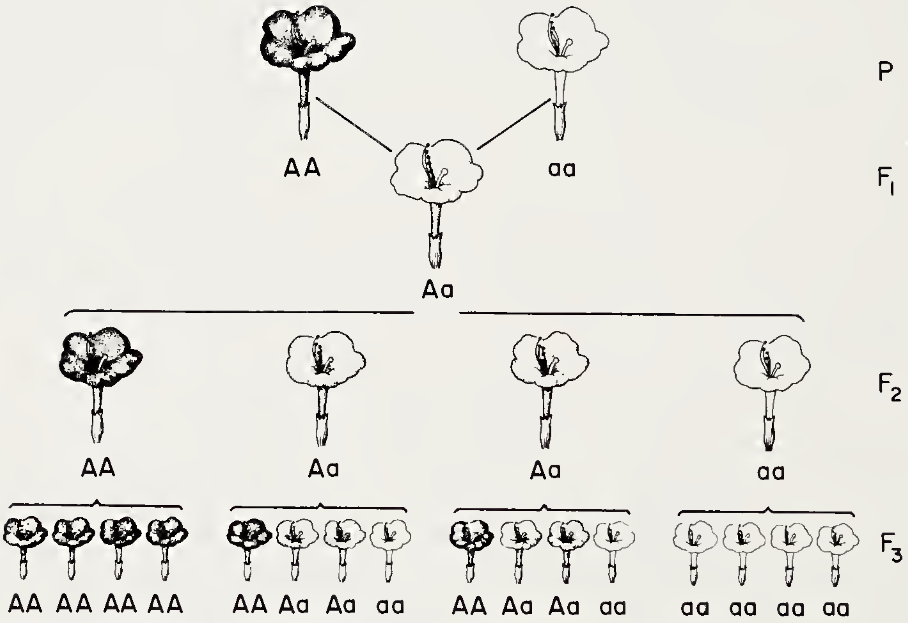

FIG. 15.1. Crossing of red and white strains of *Mirabilis jalapa* resulting in intermediate hereditary expression. *AA* alleles for red and *aa* for white-colored flowers; P, parental generation; F_1, F_2, F_3, first, second, and third filial generations. See text for further explanation. (After Correns.)

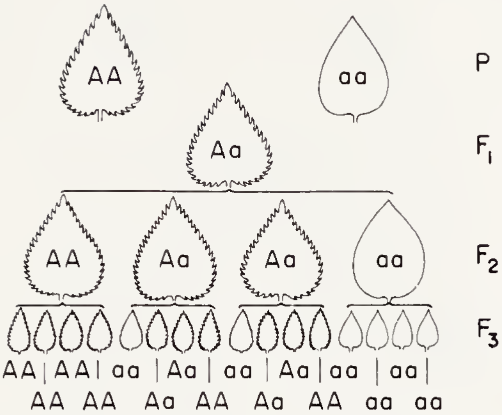

FIG. 15.2. Crossing between *Urtica pilulifera* (alleles *AA*, dentate leaves) and *Urtica dodartii* (alleles *aa*, straight-margined leaves) with a dominant hereditary process. The "dentate" allele is dominant. (After Correns.)

Segregation

When F_1 monohybrids are crossed, the members of the F_2 generation are not alike. With an intermediate type of heredity there appear many individuals, apart from those with hybrid characteristics, which display the characteristics of one or other of the parents, i.e., in our example *Mirabilis jalapa* plants with red or white flowers besides those with pink ones. When these experiments are carried out on a larger scale, permitting a statistical evaluation of the results, the ratio of 1:2:1 is obtained, i.e., 25% of plants with red, 50% with pink, and 25% with white flowers (Fig. 15.1.) This distribution is caused by the fact that the *gametes corresponding to their haploid character, can contain only one of the two alleles*, i.e., either *A* or *a;* zygote formation can therefore give rise to the combinations *AA*, *Aa*, *aA*, or *aa*. However, since *Aa* and *aA* are identical with respect to their phenotype, the numerical ratios given above are produced. The gametes, therefore, have no hybrid character and *the segregation principle is also known as the rule of the purity of the gametes.*

Basically the same holds true for the dominant type of hereditary process. In this case, however, the hybrids are similar to one of the parents, and the phenotype ratio is therefore 3:1 (Fig. 15.2). With respect to the genotype, however, the ratio *AA*:*Aa*:*aa* is still 1:2:1. This shows up in the F_3 generation.

The question whether externally similar individuals are pure strains or hybrids can be decided by back-crossing with the recessive parent (Fig. 15.3). If the individuals are pure strains with the homozygous gene pair *AA*, then the F_1 generation resulting from the back-crossing (to *aa*) is

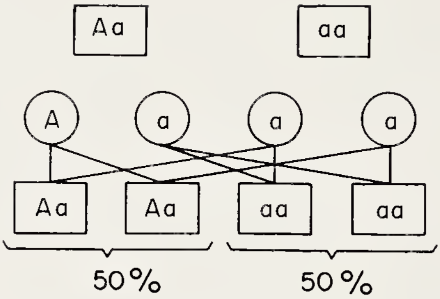

FIG. 15.3. Back-crossing of a monohybrid with the recessive parent (schematic): *A*, dominant; *a*, recessive allele.

uniformly *Aa* and is therefore similar with regard to phenotype to the dominant parent. If, however, the individuals are heterozygous monohybrids, *Aa*, then only 50% of the products of the back-crossing will exhibit the phenotype of the dominant parent, which are wholly monohybrids themselves, while the other 50% will be like the recessive parent, i.e., homozygous.

Rule of the Recombination of Genes or Independent Assortment

When strains differing with respect to two or more alleles are crossed, (dihybrid cross) the individual alleles are inherited independently of each other; each allelic pair follows the distribution given by the second of Mendel's laws. The various alleles may therefore freely combine with each other. Consider, for example, two varieties of the snapdragon (*Antirrhinum majus*) which differ in two allelic pairs. One has white and dorsiventral and the other has red and actinomorphic flowers; the alleles for white and actinomorphic are recessive, while those for red and dorsiventral are dominant. The parents therefore possess the gene pairs *aaBB* (white–dorsiventral) and *AAbb* (red–actinomorphic) and the gametes formed are *aB* or *Ab*. The F_1 generation is then, corresponding to Mendel's first law of dominance of the alleles, uniformly red–dorsiventral with the formula *AaBb* (Fig. 15.4). *Due to the independent assortment of allelic pairs, the hybrids of the* F_1 *generation can form the following gametes: AB, Ab, aB, and ab.* It can be seen from the recombination square (Fig. 15.4) that fusion of the gametes to form the zygote yields 16 possible modes of recombination altogether; these are partly hybrids again, and partly homozygous individuals. The latter are marked on the recombination square by the squares bounded by thick lines along the diagonal. The 16 recombinations belong to four phenotypes in all; two of these, i.e., white–dorsiventral and red–actinomorphic, are similar to the

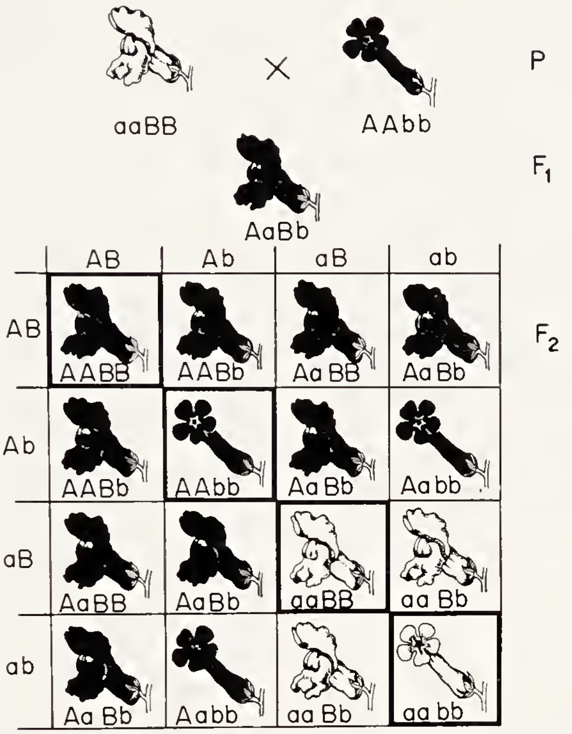

FIG. 15.4. Crossing of two varieties of the snapdragon (*Antirrhinum majus*) with the following alleles: flowers white (*aa*, recessive), dorsiventral (*BB*, dominant); and flowers red (*AA*, dominant), actinomorphic (*bb*, recessive). The F_1 generation is uniformly red–dorsiventral, while the F_2 generation is divided, as shown in the recombination square, in the ratio 9:3:3:1. [After Baur (1930).]

parents while the other two, i.e., white–actinomorphic and red–dorsiventral are fresh combinations. The four phenotypes occur in the ratio 9:3:3:1 (Fig. 15.4). The possibility of recombination of the genes therefore allows the breeding of new varieties.

COUPLING OF GENES

Free combination of genes is explained by the arrangement of the respective genes in the various chromosomes. The recombination takes place during meiosis (see p. 269). In this process the homologous chromosomes are divided into each daughter cell genome at random, and not according to their provenance from the paternal or maternal genomes (independent assortment).

Since each chromosome as a rule carries several genes, the free combinability of genes must have certain limits. It has in fact been shown that some genes are inherited in pairs (coupling of genes). The number of identifiable coupled groups corresponds to the number of chromosomes in a genome.

EXCHANGE OF GENES

There are, however, exceptions even to the principle of gene coupling; a gene or a group of genes coupled in a quite distinct gene group may suddenly appear in a wholly different combination. This is explained by the exchange of segments known as *crossing over* (see p. 269). The exchange is between the segments of homologous chromosomes; in heterozygous organisms this is bound to result in a recombination or "recoupling" of genetic factors. Thorough study of the exchange of factors has greatly increased our knowledge of the localization of genes on the chromosomes. The arrangement of genes on the chromosomes is linear, and thus the probability of an exchange between two pairs of genes increases with increasing separation along the chromosome (Fig. 15.5). The arrangement of the genes on chromosomes can therefore be approximately inferred from the tendency of selected gene pairs for exchange. In this way it has proved possible to produce quite accurate chromosome charts for some well-investigated experimental objects.

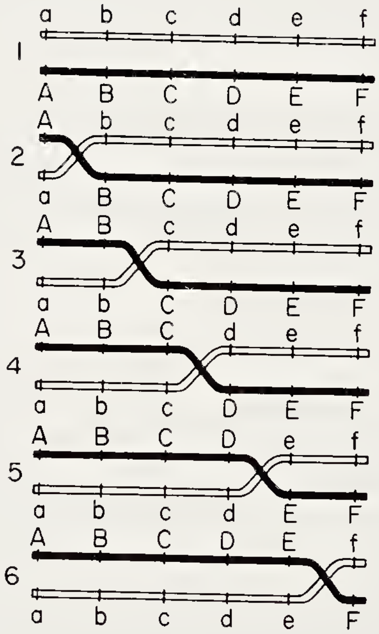

FIG. 15.5. Explanatory scheme for the exchange frequency of a chain of genes. [After Kuhn (1961, p. 94).]

RECOMBINATIONS IN BACTERIA

Bacteria have proved to be particularly suitable objects for the study of the arrangement of genes in chromosomes. When it was found that crossing, i.e., recombination of characteristics, is possible in some bacteria in spite of the absence of a sexual act (cf. p. 266), they soon became the standard experimental material in genetics. The reason for this is that they produce an enormous number of offspring in a very short time and also that they seem to contain only one "chromosome" (see p. 104). The recombination can be illustrated on two strains of *Escherichia coli* that have lost their ability to synthesize the amino acids leucine (L^-) and methionine (M^-). When these strains are inoculated onto a so-called minimal medium[1] containing neither leucine nor methionine, no growth occurs (Fig. 15.6). If, however, the two strains are mixed before inocula-

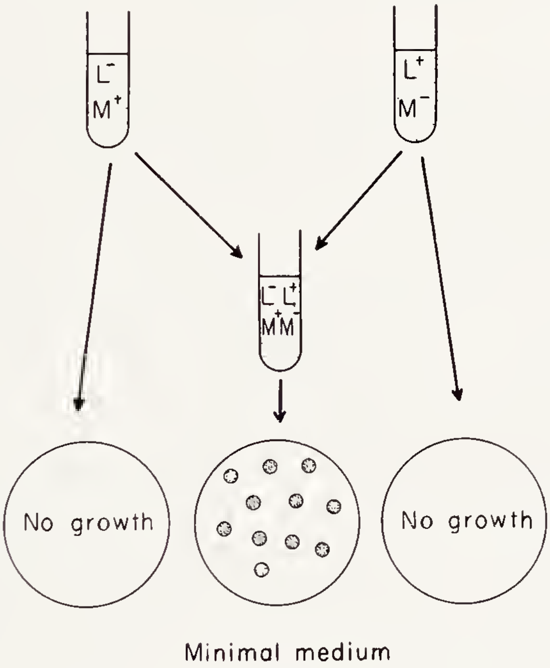

FIG. 15.6. Recombination in bacteria. The L^- strain cannot synthesize leucine and the M^- strain cannot synthesize methionine. Neither will grow on a minimal medium containing neither leucine nor methionine. When the two strains are mixed, recombinations occur which will grow on the minimal medium, i.e., which can synthesize both amino acids. [After Kuhn (1961, p. 188).]

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[1] Bacterial culture can either be carried out in liquid or on solid growth media stiffened by agar agar, a polysaccharide extracted from red algae. This is added to the nutrient solutions in small quantities (1–2%) and is dissolved by heating. On cooling it stiffens into a gel on which single germs can be made to develop in isolation from one another.

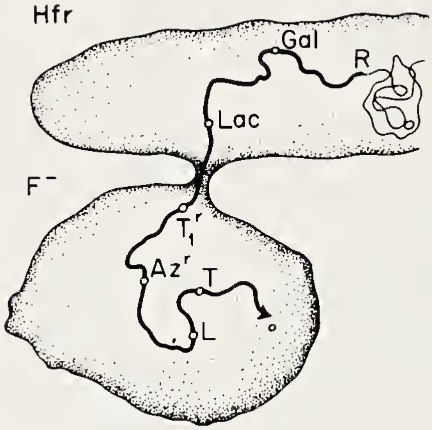

FIG. 15.7. Schematic transfer of the lineome from the donor Hfr to the acceptor F⁻ in *Escherichia coli,* strain K12. Circles marked with letters and numbers give the location of individual genes. (After Kaudewitz.)

tion, then some colonies do develop on the minimal medium and can apparently synthesize both amino acids; they therefore correspond to the original "wild" form. Recombination must therefore have taken place between some individuals.

Since direct contact between individuals belonging to the two strains is essential if the recombination is to take place, it must be assumed that the transfer of genes occurs by conjugation, i.e., by the formation of a link between plasmas which is comparable to a sexual act. In some cases it has been possible to identify conjugating bacteria in the electron microscope. As has been shown schematically in Fig. 15.7, the lineome[2] or a part of it is transferred through a narrow bridge of plasma from the donor to the receptor. If the transfer, which requires a certain length of time for completion, is interrupted prematurely at various intervals after the start of the conjugation, the arrangement on the lineome can be inferred by determining the genes already transferred to the receptor.

Chemical Nature of Genes

The carrier of genetic information, the genetic material, is typically DNA. Owing to its structure it possesses the essential characteristics necessary for the transfer of genetic information: (1) a high specificity based on a specific nucleotide sequence (see p. 21), enabling it to initiate

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[2] The arrangement of genes in the chromosomes is linear; this arrangement is therefore known as a lineome (see p. 103).

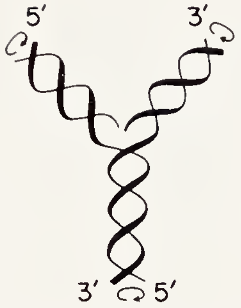

Fig. 15.8. Scheme of DNA replication. Cleavage of the two strands and synthesis of complementary strands. [After Delbrück and Stent (1957) from Wittmann.]

a very specific reaction which in turn leads to the formation of quite specific material; and (2) the ability for self-replication, i.e., the ability to reproduce identical DNA molecules.

The reproduction of identical DNA molecules occurs probably by separation of the two helical strands followed by reformation of the missing, complementary, strands (Figs. 3.10D and 15.8). The nucleotides, whose synthesis has already been discussed (see p. 241) and which undergo specific coupling, arrange themselves into single strands and are joined into chains with the aid of DNA polymerases.[3] DNA synthesis is possible only when a chain of nucleotides is already present as an initiator, upon which the nucleotide units may then line up. The chain then synthesized exhibits the complementary nucleotide pattern. As both native DNA strands synthesize the complementary partners, the process ends with two complete DNA molecules. As a result of the counterrotation of the two strands (see Fig. 1.7), the polymerization of one of the strands starts from the 3′ and that of the other from the 5′ end (Fig. 15.8). Since *in vitro* DNA polymerase synthesizes the DNA strands only from the 3′ end, it is assumed that other enzymes also play a part in the process.

The assumption that the genetic material is normally DNA was made already at a time when the structure of the DNA molecule was wholly unknown. This was supported, among other things, by the regular occurrence of DNA in cell nuclei, accurate distribution of chromosomes containing DNA in mitosis, constancy of the DNA content of diploid, somatic nuclei from different tissues of one and the same organism, etc. Experimental proof was first obtained only in 1944 by Avery, who succeeded in transferring the DNA of virulent *Pneumococcus* strains forming mucous capsules (the so-called S forms) into nonvirulent R forms forming no

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[3] Kornberg and Ochoa have been awarded the 1959 Nobel prize in medicine for the elucidation of the synthesis of nucleic acids and their role as information carriers.

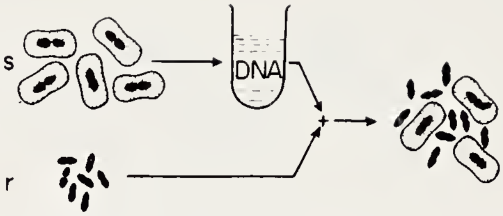

FIG. 15.9. Schematic transformation in pneumococci. r, Rough; s, smooth forms. [After Kaudewitz (1957).]

capsules, transforming the latter into the former (Fig. 15.9). This process of direct transfer of DNA is described as *transformation*. The transformed bacteria retain the new properties of virulence and capsule formation and pass them on to their offspring.

BACTERIOPHAGES

Even more impressive results confirming the role of DNA as the genetic material have been obtained in experiments with bacteriophages, the viruses of bacteria. Bacteriophages can be divided into a head and a tail region (Fig. 15.10A). The head is globular, cylindrical, or polyhedral and has a diameter of 500–1000 Å. It consists of a protein shell enclosing a cavity in which is normally found a strand of DNA. Recently, however, phages containing RNA have also been found. The tail is a hollow cylinder and also consists of proteins; the phage attaches itself to the cell walls of bacteria by means of this tail (Fig. 15.10B,C). The proteins are specific for certain receptor sites on the bacterial walls, and this explains the specificity of phages for certain bacteria. The tail cavity is enclosed by a protein layer which apparently causes local dissolution of the bacterial cell wall and thus enables the DNA filament to penetrate the bacterial cell (Fig. 15.10D,E). The fact that only the DNA penetrates, and not the protein, can be demonstrated very elegantly. The shell protein of the phage may be labeled with radioactive sulfur (^{35}S) and the DNA with radioactive phosphorus (^{32}P).[4] It can then be shown that only the nucleic acids with labeled phosphate have penetrated the bacteria, while the protein shells labeled with sulfur can easily be separated from the bacteria. The genetic information contained in the DNA molecule having entered the cell compels the infected bacterium to synthesize both the DNA and the shell protein of the phage instead of its own body substances (Fig. 15.10F,G).

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[4] Neither of these elements is present in both the DNA and the protein.

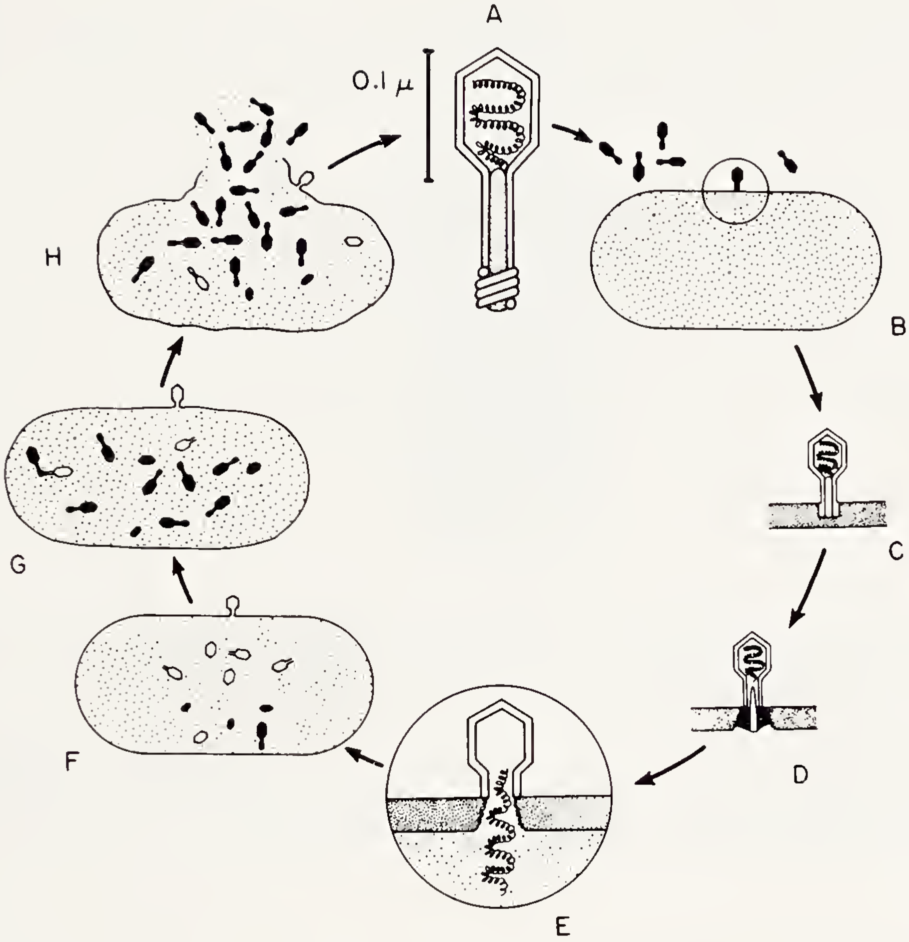

FIG. 15.10. Schematic propagation cycle of a virulent phage. (A) Phage, strongly magnified; (B)–(C) adsorption of the phage on the bacterial cell wall; (D) perforation of the cell wall; (E) injection of DNA; (F)–(G) phage synthesis; (H) lysis. [After Kaudewitz (1957).]

Thus, it has been proved that DNA may induce the synthesis of a protein. In the ripening stage further infectious phages are produced (about 100–1000 per bacterial cell) which are released on dissolution of the bacterial cell (lysis) and are ready to infect other bacteria (Fig. 15.10H).

The propagation of the phages is a rapid process and so is the infection and lysis of bacteria, giving rise to holes (plaques) in otherwise homogeneously growing bacterial colonies. The appearance of these holes is characteristic of the individual phage types (see Fig. 15.14) and can be utilized as a genetic characteristic in crossing experiments. If, for example, some members of a bacterial population are resistant to a phage while some others are not, the resistant bacteria survive and the holes appear turbid;

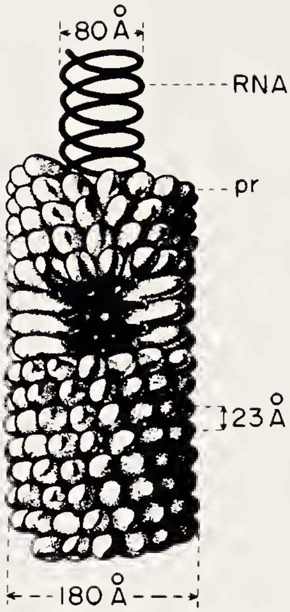

FIG. 15.11. Schematic model of the tobacco mosaic virus. pr, Protein subunits. [Adapted from Franklin, Caspar, and Klug, from Wittmann (1960).]

the appearance of clear holes indicates that no members of the population are resistant to the infecting phage. The size of the holes formed in a given time can also serve as a useful characteristic.

VIRUSES

There are many types of viruses which show that not only DNA, but also RNA can act as a carrier of information. For example, this is the case with all plant pathogenic viruses which appear isodiametric or rod-shaped in the electron microscope. The tobacco mosaic virus (TMV) is the best investigated type and can be used here as an example. It is rod-shaped, 2500–3000 Å long and 150 Å in diameter. Its particle weight[5] amounts to about 40 million. As shown in Fig. 15.11, the RNA macromolecule is helical with over 2000 protein subunits (all alike) lined up along the helix. Each subunit consists of 158 amino acids, the sequence of which is known. The protein shell, which accounts for about 95% of the virus particle, is not continuous, but contains holes 50–60 Å in diameter, which allow access for smaller molecules to the inside of the protein tube. The RNA helix, which has a diameter of 80 Å, consists of about 6000 nucleotides;

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[5] The term "molecular weight" is often used but is incorrect, since viruses are associations of numerous large molecules and not single macromolecules.

these are arranged along a single strand. To replicate it, the host cell must therefore first produce a complementary strand; the replication is then accomplished on this template. The propagation of single-stranded nucleic acids therefore also proceeds by way of double strands.

When TMV penetrates a cell of a tobacco plant, it is bound closely to the cell structures and directs the cell to synthesize virus RNA and virus protein. The virus, like the bacteriophages, is therefore propagated by the host cell; this finally leads to the development of the characteristic mosaic symptoms. The protein shell may be decomposed by treatment with phenol, leaving only the nucleic acid strands behind. The infecting power is not lost in the process, which shows that in TMV, too, the information is transferred solely by the nucleic acid, which the protein shell serves merely to protect the extremely sensitive nucleic acid strands.

Both the bacteriophages and viruses are closely linked to the cell structures while in the host cell and induce the host to reproduce the virus nucleic acids exactly and also to put their genetic information into effect, i.e., they induce reactions leading to the formation of virus proteins. Their properties are therefore the same as those characteristic of genetic material. Viruses and bacteriophages can therefore be regarded to a certain extent as self-contained genes. Thus the argument whether or not viruses are live organisms also becomes superfluous. A gene, which is an integral part of a genome, would not be called an independent organism; the same should hold for transferable genes or groups of genes.

Lysigenous Cycle

The game character of bacteriophages is manifested even clearer in the the so-called lysigenous cycle. Not all phages induce the infected cells at once to produce phages. Tempered phages are also known, which attach themselves as prophages to the lineome of the infected bacterium, where they are propagated simultaneously in subsequent divisions of the bacterium which is then described as lysigenous (Fig. 15.12). The phage may then suddenly become virulent, either spontaneously or as a result of external stimuli and induce the bacterium to produce phages leading finally to lysis. The phage therefore behaves like a bacterial gene, which determines the characteristic of phage synthesis; it is passed on from generation to generation and finally it is put into effect.

Transduction (Fig. 15.13)

Apart from the gene determining "phage synthesis," which is responsible for the lysigenous cycle, bacteriophages may transfer other genes as

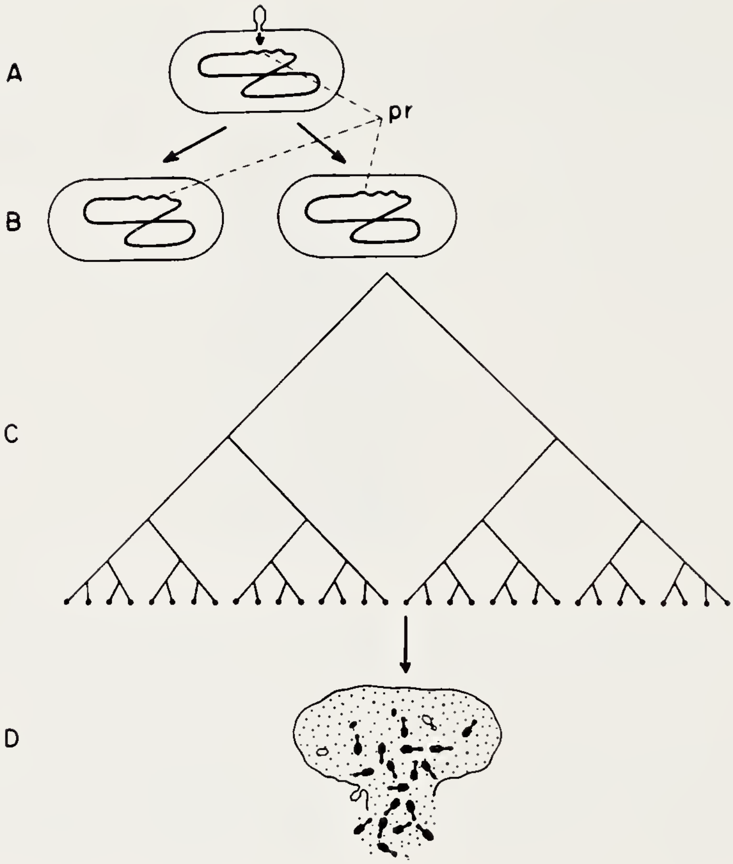

FIG. 15.12. Schematic lysigenous cycle. (A) Infection with a tempered phage; (B)–(C) cell divisions with simultaneous reproduction of the prophage (pr); (D) lysis; the phage is built into the ring-shaped bacterial lineome tangled up inside the bacterial cell.

well. This process is known as transduction. The gene determining "toxin resistance" may serve as an example. The term toxin stands here for any bacterial inhibitor, e.g., an antibiotic (see p. 327). Two bacterial strains, one of which is resistant to a particular inhibitor and the other is not, may be inoculated into a medium containing the inhibitor. The first strain will grow, while the second will not. Next a suitable phage is transferred to the culture of the bacterial strain resistant to the toxin; this strain will act as the donor of the gene controlling toxin resistance. The phage is then allowed to propagate. Next, the phage is separated from the bacterial culture by filtration through a microfilter (phages pass such filters without difficulty) and the filtrate containing the phage is allowed to act on the receptor strain sensitive to the toxin. If some of this mixture is then transferred to a growth medium containing the toxin, a number of colonies

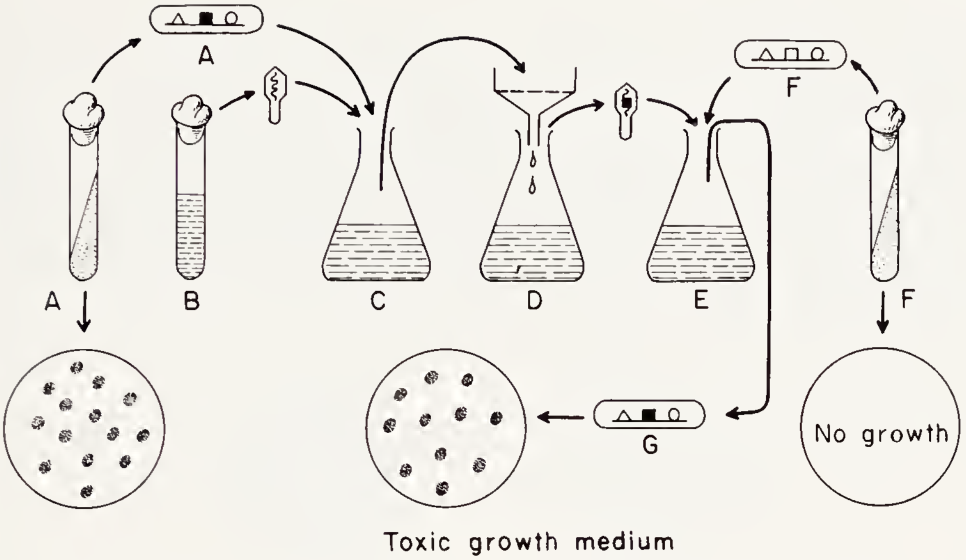

FIG. 15.13. Schematic transduction. (A) Bacterial strain resistant to toxins, which functions as donor of the "toxin resistance" gene; (B) phage strain functioning as vector; (C) propagation of the phage inside the donor; (D) separation of the donor by filtration; (E) transfer of the gene controlling "toxin resistance" by the phage to the toxin-sensitive receptor (F); (G) transduced strain growing on the medium containing toxin.

will appear, showing that the gene responsible for toxin resistance has been transferred from the donor to the receptor. The section of the lineome transduced by the phage may include more than one gene. It is not yet clear, however, whether in all these cases the phage functions merely as a transferring agent (vector) of genes or whether, as happens with the tempered phages, they can also represent integral constituents of the phage.

RECOMBINATION IN PHAGES

The attribution of gene character to viruses and bacteriophages in the preceding discussion does not mean that a virus or phage particle is equivalent to a single gene. On the contrary, it has already been shown that certain phages contain several genes. Phage strains pathogenic toward the same bacterium, but whose genes differ, can also be crossed, and recombinations can thus be obtained by effecting a double infection. If, for example, one of the phage strains produces small, clear holes in a bacterial colony, while another produces large and turbid holes (see p. 299), then a doubly infected bacterium will reveal after lysis not only holes of the "parent" type (i.e., small–clear and large–turbid ones) but also recombinations (i.e., large–clear and small–turbid) (Fig. 15.14). The recombinations take place during the vegetative phase of the phage, while the phage DNA is accurately reproduced. The recombinations occur by an exchange of genes between the DNA strands of the two phages, which in principle corresponds to the crossing over of homologous chromosomes. Here too one can therefore infer the gene arrangement from the frequency of recombinations, and thus determine the position of the genes on the phage lineome.

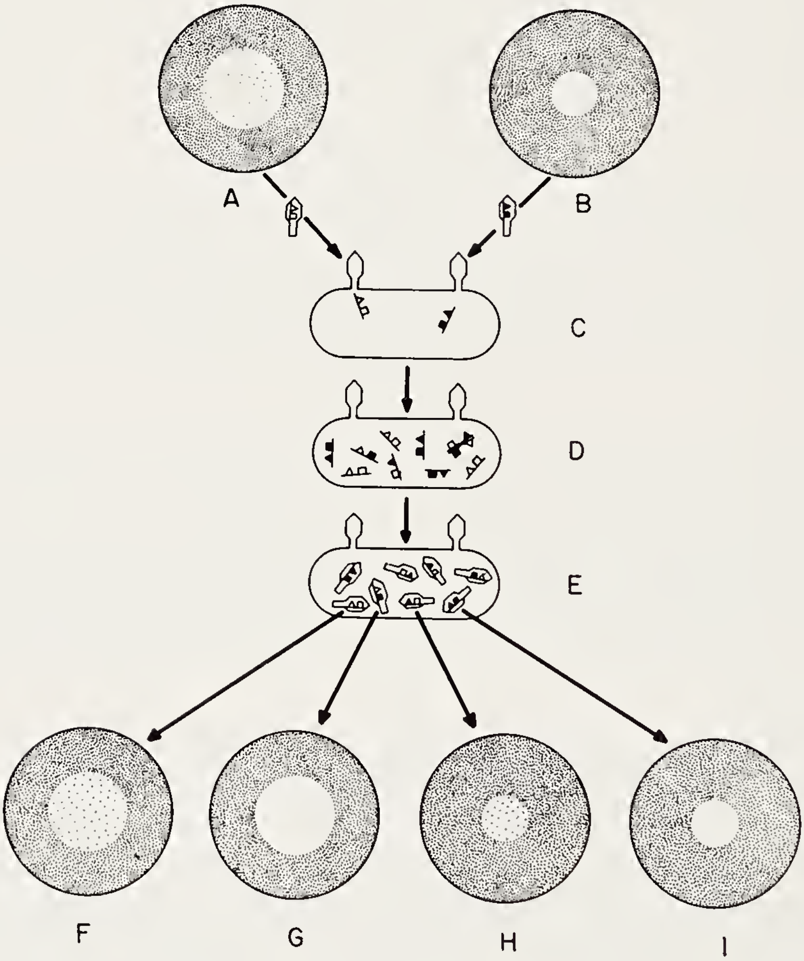

FIG. 15.14. Recombination in bacteriophages: After double infection (C) of a bacterium with a phage strain of the "large-turbid" type (A) and one of the "small-clear" type (B), the recombination products "large-clear" (G) and "small-turbid" (H) appear along with the original types (F, I) during the vegetative phase (D, E). The recombination products arise by an exchange of genes. Further explanation in text.

Mutations

In some cases discussed so far the new inherited properties have always appeared as a result of the transfer or recombination of genes that were already available. The passing on of these genes without alterations has been regarded as one of the characteristic properties of genes. However, such constancy is not absolute: the genes can undergo changes, known as mutations, which are then inherited. The origin of strains that differ only with respect to a few characteristics, or even one, can itself only be explained by the occurrence of mutations. Three types of mutations are normally distinguished—genome, chromosome, and gene or point mutations—although the boundaries between these types are sometimes unclear.

GENOME MUTATIONS

Genome mutations are those in which the number of chromosomes in a set is altered, while the structure and the gene content of the chromosomes remain unchanged. The most striking example of genome mutation is polyploidy, which involves a doubling or multiplication of the chromosome sets (see p. 64). Polyploid organisms arise when the reduction of the number of chromosomes in meiosis fails to take place giving rise to diploid gametes which fuse to yield a tetraploid zygote. When one of the two gametes is normally haploid, the resulting organism is triploid. Individuals with 4, 8, and more chromosome sets can arise in this way (Fig. 15.15).

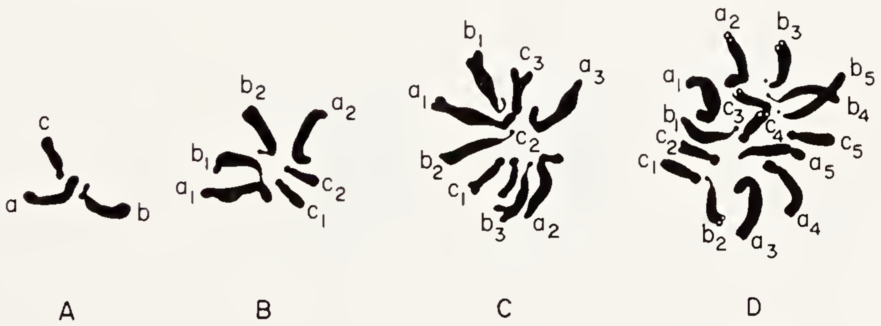

FIG. 15.15. Polyploidy in *Crepis capillaris*: (A) haploid; (B) diploid; (C) triploid; (D) pentaploid sets. The homologous chromosomes are marked with similar letters a_1, a_2, etc.). (After Hollingshead and Navashin.)

Such polyploid plants are frequently produced in nature, but they can also be produced artificially (see below). Among cultivated plants, wheat, oats, potatoes, and others are polyploid. The polyploid forms are often larger, more resistant, more productive, and are therefore of great value in plant breeding. In the meiotic divisions of plants which possess an odd number of chromosome sets (triploids, pentaploids, etc.), and also following the action of mutagenic agents and radiation (see below), the division of chromosomes between the daughter cells is irregular (aneuploidy); such organisms usually do not develop normally.

CHROMOSOME MUTATIONS

These mutations lead to changes in the structure of chromosomes, i.e., to changes in the arrangement of the genes on the lineome. They can often be recognized microscopically by comparison with unaltered, homologous chromosomes. The occurrence of chromosome mutations depends on chromosome fragmentation; this can also be caused artificially (see below). As can be seen in Fig. 15.16, the fragments can become lost (deletion) or attached to other chromosomes (translocation). The attachment may occur to the corresponding section of the homologous chromosome (duplication). If, on the other hand, the fragment is reversed before it is reinserted into the same chromosome, the process is one of inversion.

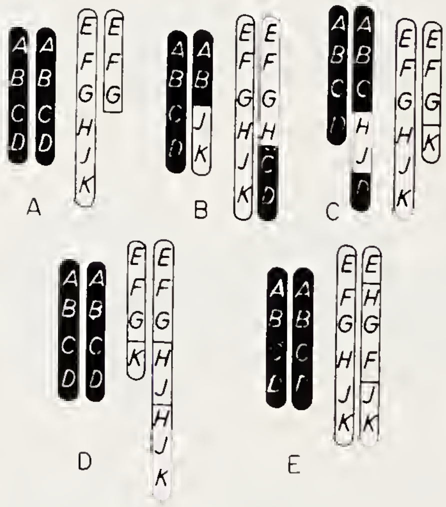

FIG. 15.16. Chromosome mutations, schematic: (A) loss of fragments (deletion); (B) reciprocal translocation; (C) unilateral translocation; (D) doubling of a chromosome section (duplication); (E) inversion of a chromosome section. [After Kühn (1961, p. 124).]

Since in the latter case changes may occur in the development of certain characteristics, even though the gene content of the cell remains unaltered, it must be concluded that the development of characteristics depends not only on the availability of the genes but also on their position in the chromosomes (position effect).

It should be mentioned at this point that reciprocal translocation of chromosome sections has nothing to do with crossing over; it is not associated with meiosis, and the participants are not homologous chromosomes.

GENE MUTATIONS

Last, the individual genes can also undergo mutations: Changes may occur in the DNA chain of a gene either spontaneously or under the influence of external factors. These cause changes in only one characteristic and cannot, as a rule, be identified microscopically as the chromosome structure is not visibly altered. Normally only one of the alleles of a pair of homologous chromosomes mutates; diploid cells thus become heterozygous. Gene or point mutations may be the only true mutations and genome and chromosome "mutations" may better be referred to as polyploids and chromosomal aberrations, respectively.

Mutations can occur spontaneously or they can be brought about experimentally. The incidence of spontaneous mutations (the rate of mutation) is normally small, varying between 0.005 and 0.00005%, but it can be increased significantly by the use of mutagenic agents or radiation.

While the mutagenic effects visible in the microscope or identifiable in genetic experiments have been well studied, our knowledge of those produced by changes in the DNA molecule is limited.

In principle, there are several possibilities. For example, the hydrogen bonds between the two strands may be broken by stretching. If, however, more than 10 successive bonds are broken, the DNA molecule is irreversibly denatured. The breaking of a phosphate ester bond is also a possibility. This, like the breaking of hydrogen bonds, would allow the removal of parts of the DNA strand, which could then be inverted and reinserted or become attached to another strand. These processes would be analogous, on the scale of the DNA molecule, to those already discussed in connection with chromosome mutations (see above). The breakage of bonds between bases and sugars is, however, impossible under biological conditions. On the other hand, the base molecules could alter along with changes in the nucleotide sequence.

ARTIFICIAL MUTANTS OF TMV

By treatment with nitric acid of appropriate pH, the RNA of the TMV can be freed from proteins. It has in fact become possible to produce infectious mutants (nitrite mutants) in this way; these can cause symptoms on tobacco leaves which differ from those caused by the normal TMV strains. The nitric acid treatment converts the bases adenine, guanine, and cytosine into hypoxanthine, xanthine, and uracil by deamination, i.e., by the substitution of NH_2— groups with —OH. Since hypoxanthine is more like guanine than adenine with respect to hydrogen bonds, guanine replaces adenine in the nucleotide strand in the subsequent coupling of bases. Nitric acid treatment therefore produces TMV mutants which have guanine in place of adenine in one position in the nucleotide chain. The position is similar with regard to the transformation of cytosine into uracil. On the other hand, the transformation of guanine into xanthine does not seem to produce mutations. In many of these mutants, though not in all, the amino acid composition of the protein subunits was found to vary. It is therefore proved that the host cell can be induced to synthesize an altered protein molecule by changing the base sequence of the RNA molecule; in other words, an artificial alteration of the genetic information of the virus alters a characteristic, i.e., causes a mutation. The change in the composition of the protein occurs only in some of the mutants, and it can therefore be concluded that only one section of the TMV nucleic acid molecule is responsible for the protein formation, while the remaining part governs other processes in the host cell which include the development of pathological symptoms. These mutations, which are caused by the alteration of the nucleotide units of the RNA in TMV, can be regarded as models for gene mutations in other organisms, even if DNA is involved. Mutants can also be produced by other compounds, e.g., by hydroxylamine.

MUTAGENIC RADIATION

All ionizing radiations have mutagenic effects, and so have the nonionizing ultraviolet (UV) rays. Nonionizing radiation, if it is to be active, must be absorbed by compounds of very specific structure (see p. 204), while the action of ionizing radiation on molecules is direct and nonspecific. Ionizing radiation may remove an electron from one of the atoms in the molecule and thus convert the atom into a reactive ion, or it may raise the electron to a higher energy level (see p. 4). Free radicals, peroxides, and other very reactive compounds can arise in this way, which then act on their environment and may produce characteristic alterations. Thus, the affected atom need not necessarily be part of the DNA strand itself. The changes brought about in cells in this way are often lethal, especially when the radiation acts over a long time, but viable mutants can also be produced, which have lost the ability to synthesize one or another compound. Mutagenic radiation causes not only gene mutation but also produces changes in the chromosome structures by way of fragmentation; these then correspond to changes described as chromosome mutations or chromosomal aberrations.

MUTAGENIC AGENTS

Similar effects can be obtained using certain chemicals (mustard gas, ethylmethanesulfonate, ethylenimine, etc.); these chemicals are therefore known as radiomimetics. Many of them act as early as the interphase, without, however, the changes brought about by them becoming visible at once. The defects in the chromosomes become evident only at the end of the prophase.

The mode of action of the metaphase or spindle apparatus toxins is quite different; examples of such compounds are acenaphthene, hexachlorocyclohexane, and especially colchicine which occurs in the meadow saffron (*Colchicum autumnale*). If one of these is allowed to act on cells during division, the division proceeds undisturbed as far as the metaphase. Then, however, the distribution of chromosomes between the poles is disturbed due to suppression of the spindle apparatus. The chromosomes remain in the equatorial plane, and restitution nuclei can arise with twice the normal number of chromosomes. Polyploid organisms can thus be produced (see above). The spindle need not always be wholly suppressed. Sometimes only some of the threads of the spindles are put out of action, so that single chromosomes remain in the anaphase. The polarity can also be disturbed, which results in the formation of more than two poles; these are the so-called multipolar spindles. This process gives rise to cells having more than one nucleus (Fig. 15.17), each of which contains a different number of chromosomes.

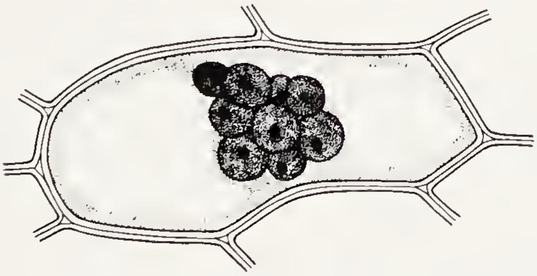

FIG. 15.17. Cell with nine nuclei from the cortical tissue of a potato root, treated with a mutagen (isopropyl *N*-phenylcarbamate) (approx. 1000×).

The mutagenic effect of nitric acid and hydroxylamine has already been discussed (see p. 308).

Mode of Action of the Genes

The experiments with nitrite mutants have shown that a change in the DNA chain can lead to an alteration in the protein structure. According to a theory known as the one-gene–one-enzyme hypothesis, each gene is responsible for the synthesis of a certain protein, mostly an enzyme protein, through which it can exercise its influence in the cell. If the gene is altered by mutation, the corresponding enzyme can no longer be synthesized and the chain of reactions comes to a halt at the stage where this enzyme should have intervened. This is described as a genetic block.

The above hypothesis has been confirmed by experiments on the most diverse organisms. An example is the synthesis of arginine by *Neurospora crassa,* one of the most important standard organisms of biochemical genetics.[6] The naturally occurring wild strain of *Neurospora* is capable of arginine synthesis. Treatment of the conidiospores with mutagenic radiation produces the biochemically deficient mutant, which is then crossed with the wild form (Fig. 15.18). The ascospores produced thereby are transferred individually to a complete growth medium, which includes the materials whose synthesis has been blocked; in our case this is arginine. Next, some mycelium from each monospore culture is transferred to a growth medium which does not contain the substance under test, i.e., arginine in this case. It can then be observed that out of eight monospore cultures derived from one ascus, four do not grow due to the blockage of biosynthesis of the substance in question, while the other four continue to grow normally. A separation of the two alleles has therefore occurred in meiosis during the formation of the ascospores, so that four of the ascospores receive the unchanged allele of the wild strain while four receive the mutant allele (Fig. 15.18H,I). The stage at which the path of synthesis has been interrupted can be ascertained by adding single amino acids to the growth medium, which could serve as arginine precursors (ornithine, citrulline) (see the reaction sequence below.) In four out of the total of seven mutants obtained, the genetic blockage is located before ornithine; they grow equally well on addition of ornithine and citrulline. The transformation of ornithine into citrulline is controlled by two genes, because two mutants can utilize citrulline but not ornithine. One of the mutants fails to grow even in the presence of citrulline, indicating that the transformation of citrulline into arginine is controlled by one gene. The reaction sequence given here is also part of the synthesis of urea (see p. 243), as urea can be cleaved off the arginine molecule by arginase with ornithine as the residue. The paths of biosynthesis have already been clarified in a similar manner for numerous compounds.

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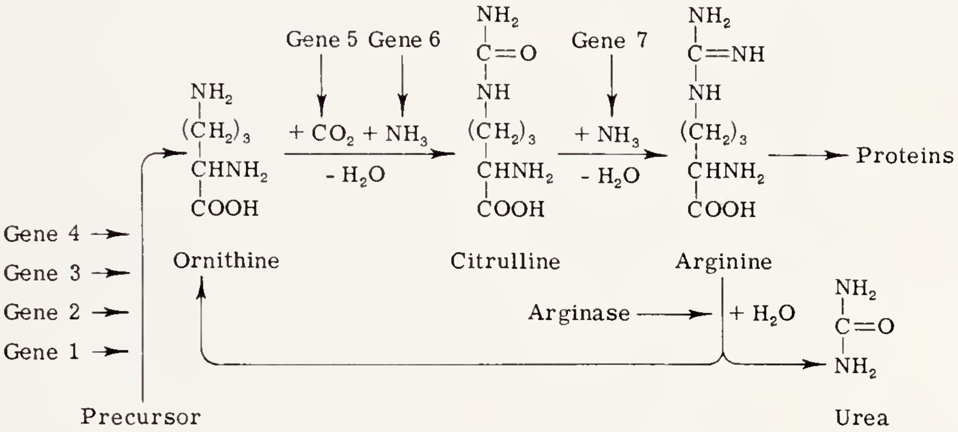
[6] G. W. Beadle together with J. Lederberg and E. Tatum have been awarded the 1958 Nobel prize in medicine for their pioneer work in biochemical genetics which has led to the one-gene–one-enzyme hypothesis.



Biosynthesis of arginine and urea in *Neurospora crassa*

PROTEIN SYNTHESIS

Since the genetic information carried by DNA is located in the nucleus and protein synthesis proceeds mainly on the ribosomes in the cytoplasm, the question arises, how is the genetic information, stored in the form of a certain nucleotide sequence, transmitted from the nucleus to the cytoplasm to be there translated into the specific amino acid sequence of a protein? This very difficult question, which constitutes one of the fundamental problems of biology, has only been elucidated in recent years. It must, however, be emphasized that our present ideas are based on studies with viruses, phages, and bacteria, and that it is still by no means clear whether, and to what extent, they can be applied to higher organisms. They can, neverthless, serve at least as models for the elucidation of the corresponding process in higher plants, and they will therefore be briefly outlined in this section.

Since DNA does not leave the nucleus, the information must be transferred by another substance. It is now known that this substance is a certain RNA fraction called *messenger RNA*. This is synthesized on DNA in the nucleus from nucleotide units, and its nucleotide sequence is com-

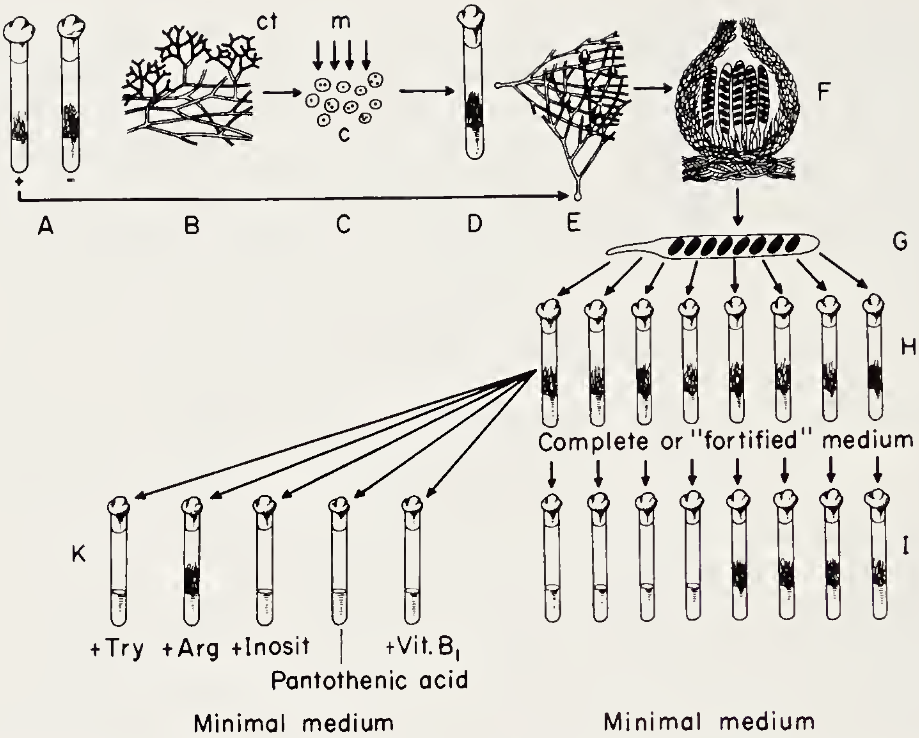


FIG. 15.18. Production and identification of biochemically deficient mutants in *Neurospora crassa*. (A) Original strains; (B) mycelium with conidium carriers; (C) irradiation of conida with mutagenic radiation; (D) and (E) crossing with wild strain; (F) perithecium; (G) ascus; (H) and (I) identification of the deficient mutants; (K) determination of the missing growth factor. c, Conidia; ct, conidium carriers; m, mutagenic radiation. (After Beadle and Kühn.)

plementary to that of the DNA; the molecule coupled to adenine is not thymine but uracil. Such "hybrid," i.e., mixed DNA–RNA strands have been identified experimentally. At the end of the synthesis, the messenger RNA strand is released from the DNA template and migrates through the pores of the nuclear membrane (Fig. 15.19) into the cytoplasm, where it attaches itself externally to the ribosomes. The length of the messenger RNA strand is extremely variable, corresponding to the protein molecules to be synthesized. They often extend over several ribosomes, which are then linked like beads on a string and are known as *polysomes* (Fig. 15.19).

The ribosomes (see p. 43) are activated by messenger RNA. Apart from the ribosomal RNA, the plasma also contains *transfer RNA* (known also as sRNA or *soluble RNA*, see p. 21), this amounts to about 10% of the total RNA in the cell. Their nucleotide chains are relatively short, consisting of 70–80 units. At the 5′ end a guanine nucleotide is normally found, while at the other end the nucleotide sequence terminates with the

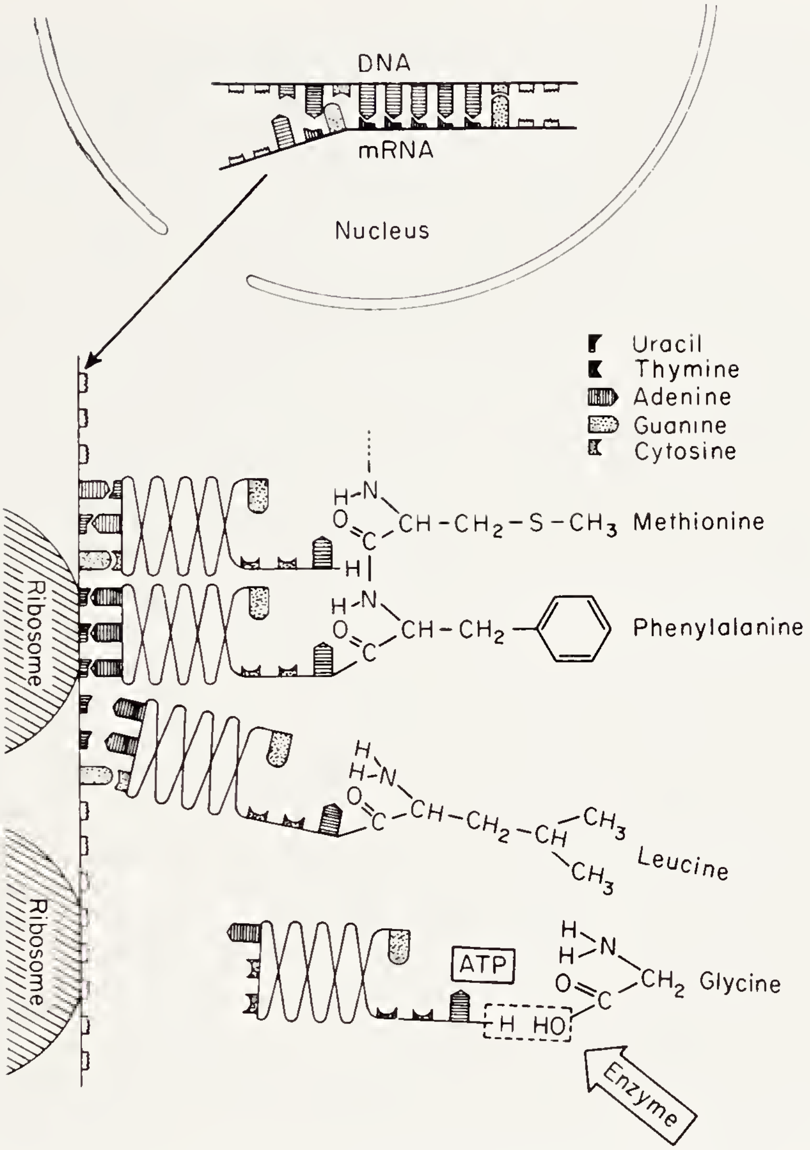


FIG. 15.19. Schematic transfer of information and protein synthesis. See text for further explanation.

bases cytosine–cytosine–adenine (Fig. 15.19). For each amino acid there is at least one specific transfer RNA, which in one of its regions (the amino acid selecting region) exhibits a specific nucleic acid sequence. The correct amino acid is then selected by means of this region from the large number of available amino acids. This molecule is then attached, through its carboxyl group (with the aid of an ATP molecule and an amino acid-specific enzyme) to the ribose molecule of the terminal adenosine with the elimination of a water molecule. The amino acid thus activated is then transported to a polysome, where the transfer RNA finds its place with the aid of another specific nucleotide sequence, the matrix-selection region. This is fixed to the messenger RNA by the always complementary nucleotide sequence. These nucleotide sequences are quite specific for each transfer RNA, and thus for each amino acid (see the genetic code), and therefore only a specific transfer RNA or amino acid can be attached to each site of messenger RNA. A peptide bond is formed between the amino group of the freshly arrived amino acid and the carboxyl group of the previously arrived one (Fig. 15.19), and the latter is released from its transfer RNA, which becomes free to transfer another amino acid molecule. The polypeptide chains are thus gradually built up, the growing amino acid chain being always connected to the messenger RNA and to the ribosome only through one transfer RNA. It can be inferred from the lining up of several ribosomes into polysomes that several protein molecules are always simultaneously synthesized on a messenger strand. The messenger RNA fixes only the primary structure (see p. 16) of the protein directly, but this seems to determine a certain secondary and tertiary structure which then develops spontaneously.

In bacteria the messenger RNA molecules are active for only short periods of time, e.g., for only about 2 minutes in *Bacillus subtilis.* During this time 10–20 protein molecules can be synthesized on one strand. This is how the synthesis ad infinitum of one and the same type of protein by the genetic information passed on to the plasma is prevented: The synthesis occurs only as long as the respective gene is active and builds messenger RNA. On the other hand, the RNA of viruses, which is comparable to messenger RNA, seems to retain its activity for much longer periods inducing the host cell to synthesize the same protein continuously. This in fact constitutes the pathogenic activity. However, the short-lived activity cannot be regarded as a typical characteristic of messenger RNA, since messenger RNA of persistent activity has been identified in other organisms as well.

THE GENETIC CODE

We are now in a position to consider the question of the genetic code, i.e., the correspondence between the above mentioned bases and amino acids. While the Morse code reproduces the 26 letters of our alphabet by using three symbols: the dash, the dot, and the interval, 4 bases or nucleotides are available for the approximately 20 biologically important amino acids. It follows from purely arithmetical considerations that for an unambiguous determination of an amino acid the minimum number of nucleotides required is three, since two nucleotides provide $4^2 = 16$, while three provide $4^3 = 64$ combinations. Although it has not yet been proved conclusively that three nucleotides, i.e., triplets, form one coding unit (codon), the assumption has proved very useful as a working hypothesis. Its correctness need not therefore be doubted. It has also been possible to elucidate the base sequences serving as code units for the individual amino acids in TMV and in the bacteriophage T4. Some examples, which have also been used in Fig. 15.19, are methionine AUG, phenylalanine UUU, leucine UUG,[7] etc. These code units apply to messenger RNA, while the corresponding regions of DNA and transfer RNA naturally exhibit a complementary base sequence. In the example shown in Fig. 15.19, the information carried on DNA, i.e., TAC AAA AAC, is transferred to messenger RNA as the sequence AUG UUU UUG. The messenger RNA migrates to a ribosome, where the transfer RNA arranges itself corresponding to the code in the sequence UAC AAA AAC; this corresponds to the amino acid sequence methionine–phenylalanine–leucine. Thus, the conversion of a certain base sequence into a certain amino acid sequence has been accomplished. The process outlined here for three amino acids does, of course, also cover polypeptides. An overlap of the code units seems to be impossible; the code is read off continuously and without interruption starting at one end. This means that the incorporation of a single additional nucleotide in the DNA strand would alter all of the subsequent information, as the nucleotide groups in the triplets would all be different. On the other hand, it appears that many amino acids may be determined by more than one codon, i.e., out of the 64 possible combinations not just 20 are meaningful but more (degeneration of the code). Whether or not the code is universal, i.e., whether all organisms use the same code units for the same amino acids, cannot as yet be ascertained, although there are many indications that this is the case.

Finally, the mode of formation of a nitrite mutant (see p. 307) with its altered protein structure will be illustrated by an example. The nitric acid treatment may transform cytosine into uracil by deamination in the code unit UCC (serine); the code unit is then transformed into UUU (phenylalanine); the protein is altered at this unit and this may lead to a change in the development of characteristics.

Selection of the Sexes

Selection of the sexes can also come about through genes (genotype sex selection). When this is not the case, the sex selection is said to be phenotypic.

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[7] A=adenine, C=cytosine, G=guanine, T=thymine, U=uracil.

Phenotypic sex selection occurs in all monoecious plants which develop male and female sex organs on the same individual. The question of which individual cell develops into the male and which into the female organ is determined here by definite (but in detail as yet obscure) physiological processes. However, these can often be guided by external factors in a certain direction, so that the experimenter may decide the type of sex organ to be developed by the organism. Phenotypic sex selection occurs both in haploid and diploid plants, and a distinction is therefore drawn between haplo- and diplophenotypic sex selection processes.

Genotype sex selection is determined by genes, as has already been mentioned. The homologous chromosomes on which the sex determining factors are located often have different shapes (sex or heterochromosomes) and are known as X and Y chromosomes. Often one type of chromosome is missing altogether; the sex chromosome is then left without a partner during the pairing of homologous chromosomes in meiosis.

In haplonts the determination of sex occurs during the germination of the zygote (Fig. 14.6B) which is coupled with a meiosis. Two of the four meiospores produced contain an X, the other two a Y chromosome (or none at all). Thus, two of the resulting individuals belong to one sex and two to the other (haplogenotypic sex selection). In reproduction, union can only occur between two gametes with opposite sex factors, irrespective of whether they are morphologically different or not.

In diplonts one of the sexes, usually the male, is heterozygous with respect to the sex-determining factors; it therefore possesses two different sex chromosomes (X and Y) or only one, while the other sex, normally the female, has two X chromosomes. The gametes of male individuals formed in meiosis (Fig. 14.6A) therefore contain 50% of X and 50% of Y chromosomes (heterogametes), while the female individuals only produce gametes with X chromosomes and are thus homogametous. Union of X and Y gametes yields a male individual, while that of two X gametes yields a female one (diplogenotypic sex determination).

In plants with an alternation of generations and dioecious gametophytes, e.g., the dioecious mosses, the sex determination process occurs during the formation of meiospores (see p. 275); half of these give rise to male and the other half to female gametophytes. However, the conditions are different for those flowering plants in which the staminate and pistillate flowers occur on different individuals (see p. 279). Here the determination of sex occurs on fusion of the egg cell (which usually contains X chromosomes) with the sperm cell. This may also contain an X chromosome, and the fusion then gives rise to a megasporophyte with pistillate flowers, or it may contain a Y chromosome, in which case a microsporophyll with staminate flowers is produced. In this instance, therefore, the sporophytes already differ with respect to their sex-determining factors in that one of them can only produce mega- and the other only microsphorophylls.

Extrachromosomal Heredity

It has been mentioned previously (see p. 290) that reciprocal hybrids are identical, but this statement is only generally true. Several instances have been discovered in which the result of a crossing depends markedly on the sex of the crossing partners. However, as the genomes are identical in reciprocal hybrids, the differences in the characteristics must be determined by extrachromosomal heredity factors.

Cytoplasmic Factors (Plasmon)

This term covers the whole of the heredity factors located in the plasma. For example, the crossing of two rose species (*Epilobium hirsutum* and *E. roseum*) results in a small, stunted and sterile F_1 generation if *E. hirsutum* is the female and *E. roseum* the male parent. In the reverse case the hybrids produced are fully developed (Fig. 15.20). The two crossings differ only with respect to the contents of the plasma of the egg cell so that the plasma must be responsible for the differences in the development of characteristics. Which of the plasma structures or enclosures act as carriers of these heredity factors is as yet obscure. Solution of this problem for *Epilobium* is difficult insofar as it is known that plastids may also influence extraplastidal characteristics (see below). Participation of the plastid heredity in the development of characteristics cannot therefore be unambiguously excluded in this case; in any case, clear separation of the cytoplasmic and plastid characters in green plants is rather difficult.

Colorless organisms without plastids are more suitable objects for this type of study. One of the most extensively studied among these is brewer's yeast (*Saccharomyces cerevisiae*). Under suitable culture conditions mutation yields yeast cells that can utilize glucose only for fermentation, but not for oxidative decomposition since they lack cytochrome oxidase. This defect is inherited in a non-Mendelian way and is therefore extrachromosomal. The carriers of the heredity factors responsible for this characteristic are the mitochondria. The role of the mitochondria DNA in this process is still unknown. It seems worth noting, however, that accord-

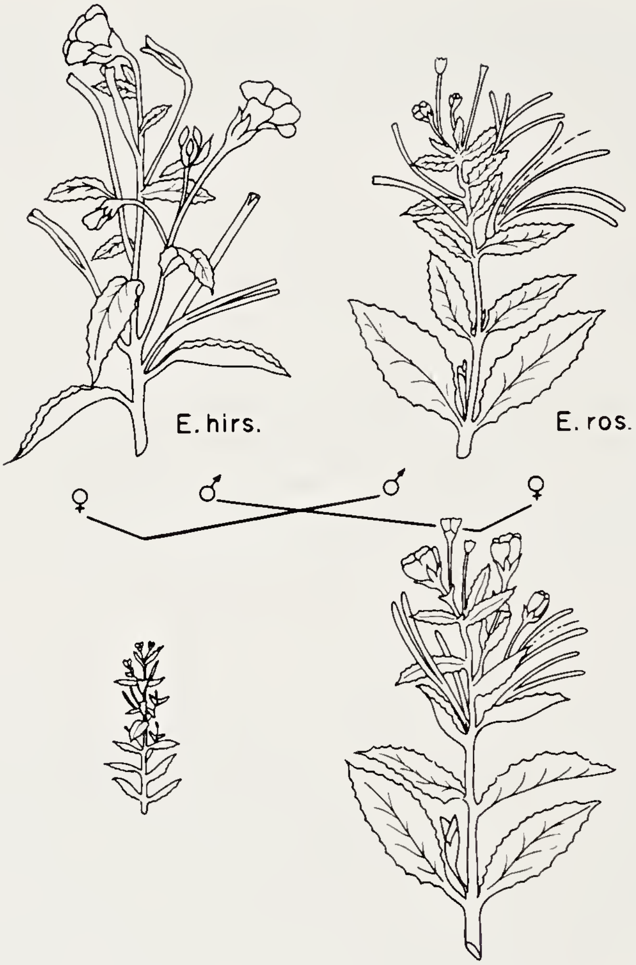

Fig. 15.20. Reciprocal hybrids of *Epilobium hirsutum* and *E. roseum*. [After Oehlkers (1953).]

ing to recent investigations the DNA of mitochondria can synthesize both RNA and proteins. This indicates that they are carriers of information in this instance as well. Yeast cells with respiratory defects can, however, also be produced by mutations of chromosomal heredity factors; the formation of active mitochondria therefore probably depends on the joint action of chromosomal and extrachromosomal heredity factors.

Plastid Factors

The situation is somewhat clearer in those cases in which the non-Mendelian behavior determines the degree of green coloration of the epigeous parts of the plant. These are cases of plastid heredity. An example is the already mentioned *Mirabilis jalapa*, the color of whose

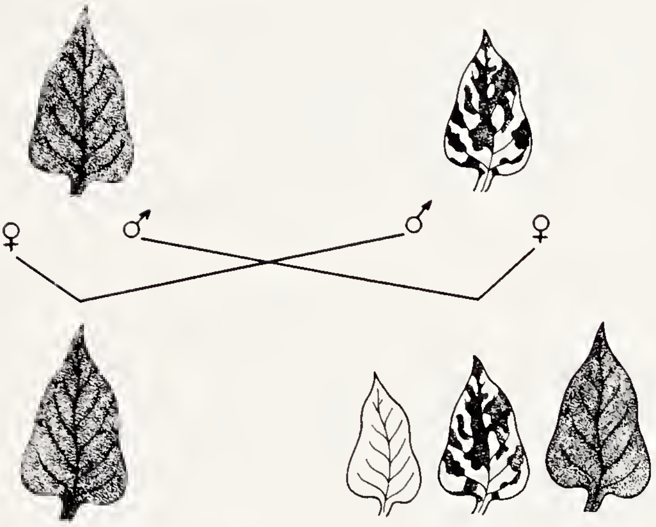

FIG. 15.21. Plastid heredity in *Mirabilis jalapa.* Crossing of ♀ green with ♂ "status albomaculatus" (white spotted variegated) yields pure green offspring, while crossing of ♂ green with ♀ "albomaculate" yields some white, some white spotted variegated, and some green offspring. [After Correns (1937).]

flowers is inherited according to Mendel's laws (see p. 289). Along with plants having pure green leaves, some white-green spotted (so-called albino-maculate forms also occur. A pure green mother may now be crossed with an albino-maculate father; the offspring are all pure green (Fig. 15.21), as the egg cell contains and transfers only normal green plastids. If, however, an albino-maculate mother is paired with a green father, some of the resulting offspring are green, some are albino-maculate, and some even quite white, depending on whether the plastids transferred by the oosphere are purely normal green, both green and nongreen, or pure nongreen. The latter are not autotrophic and normally die off. The loss of the ability to develop the green color must therefore be regarded as a plastid mutation. The whole of the heredity factors located in the plastids is known as the plastom to distinguish it from the genome and plasmon, respectively. The role of the nucleic acids of plastids (see p. 53) in these processes is still unknown.

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Chapter 16

Development

The term *development* summarizes the processes by which a germ cell, whether it has arisen by a sexual process or otherwise, develops into the final vegetative body of the plant. For convenience and detailed treatment we may subdivide development into four stages: growth, differentiation, organogenesis, and morphogenesis.

Growth is an irreversible increase of volume and mass (to distinguish it from swelling) undergone by living cells. Growth normally also leads to changes in shape and is also an integral part of many developmental phenomena. Thus, growth includes the processes of *cell division* and *cell enlargement,* and cell enlargement is an integral step in cell differentiation.

The development of the plant organisms, especially multicellular ones, includes therefore both the processes of cell division and cell growth and also those of differentiation which lead to the subdivision of cell functions and hence to the development of tissues and organs (organogenesis) which results in a characteristic size and form for the organisms (morphogenesis). The development process is guided by internal factors determined by the genetic information obtained from the parent organism; it can, however, also be modified within certain limits by external influences (light, temperature, polarity, hormones, etc.). Development is therefore a complicated set of processes, mutually determining and influencing each other, and is as yet not wholly understood.

The following discussion is a selection of some of the most important and most interesting points of view; they are, however, only components of the whole and in no way represent a balanced, complete picture of the processes summed up by the term "development."

Growth of Unicellular Organisms

At the unicellular and colony levels of organization the individuals arise mostly directly from the mother organism or from the germ cells by single or multiple divisions, and formative effects are here rather unimportant. For this very reason, however, certain phases of growth and the possibilities of influencing them can well be studied on such organisms. Favorable conditions are rapid propagation and thus the possibility of building up a large population in a relatively short time. This is why much of the information concerning growth and especially plasma propagation has been obtained using microorganisms.

THE COURSE OF THE GROWTH PROCESS

When microorganisms or their germ cells are transferred to a suitable growth medium, the number of cells begins to grow after a short preliminary phase in which the number of cells does not increase but their size does (Fig. 16.1,I). The rate of increase in the numbers of bacteria increases at first in the acceleration phase (Fig. 16.1, II), until a constant rate is achieved. If the number of cells is determined at fixed intervals in the third stage, and if the logarithms of these values are plotted as the ordinate against time, a straight line is obtained. This stage is known as the logarithmic phase of growth (Fig. 16.1, III). The number of cells rises here exponentially, i.e., one cell gives rise to two, four, eight, etc., or generally to $2n$ cells. With aging of the culture the rate of increase in the number of bacteria slows down due to exhaustion of nutrients and accumulation of toxic metabolic products—this is the retardation phase (Fig. 16.1, IV). The growth curve flattens out horizontally leading to the stationary phase (Fig. 16.1, V). The number of cells now remains constant unless a diminution (lag) phase follows (Fig. 16.1, VI), in which part of the cells die off through autolysis.

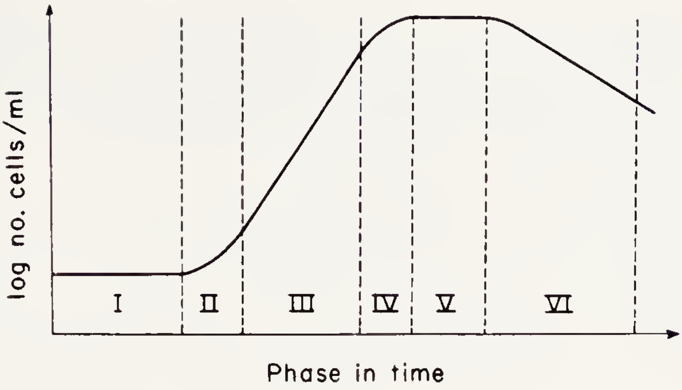


Fig. 16.1. Phases of growth of a bacterial culture (schematic): (I) preliminary; (II) acceleration; (III) logarithmic; (IV) retardation; (V) stationary; and (VI) diminution. [After Klein (1957).]

Most of the studies on microorganisms are carried out in the logarithmic phase of growth. In recent times continuous dilution techniques have been developed for this purpose, by means of which the number of organisms can be kept constant by a steady supply of fresh nutrient solution. The culture is kept in the logarithmic phase in this way. In many cases, by skillful manipulation of the experimental conditions, it is even possible to make all or nearly all organisms in the culture divide at the same time so that they are all of the same age (synchronization). It has thus become possible to study the properties of microorganisms, e.g., their composition, at various stages of growth after cell division. Such studies were not possible with normal cell cultures containing cells of all ages.

GROWTH FACTORS

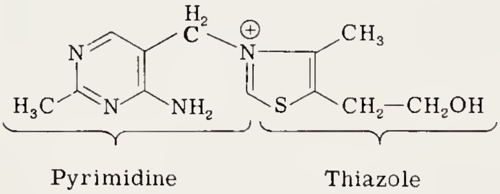
As has already been mentioned (see p. 249), some heterotrophic microorganisms require for their growth specific substances which they cannot synthesize themselves but must obtain from the environment. One class of such substances are known as vitamins. It is obvious that microorganisms are especially suitable for the study of the specific effects of such growth substances.

The role of vitamins was first discovered during the study of deficiency diseases in humans and animals (avitaminoses), e.g., the prevention of beriberi by vitamin B_1 and that of scurvy by vitamin C (ascorbic acid). Vitamins were therefore defined as active substances that are essential for the normal life of the human or animal organism but that cannot be synthesized by them. They differ from the other nutrients required by heterotrophic organisms by their marked specificity and especially by the fact that they are required only in minute quantities. These findings lead to the conclusion that the function of vitamins is not to release energy but to intervene in the more important elements of metabolism, namely enzymes.

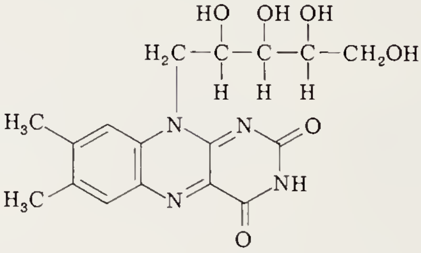
This also holds, of course, for the enzymes of the plant organism but with the difference that the autotrophic plant can synthesize these structural units itself, while the microorganisms mentioned above behave in this respect like humans and animals. Many growth factors are now known, and only a few characteristic examples will be selected here for discussion.

Thiamine (Vitamin B_1, Aneurine)

Thiamine is in its active form of pyrophosphate a component of many enzymes, among them the decarboxylases, and also of transketolase which transfers C_2 fragments (active glycolaldehyde). It is noteworthy that the needs of the microorganisms requiring this vitamin vary greatly. Thus, the fungus *Phycomyces blakesleeanus,* used as a test organism for thiamine, can grow even when the two components of thiamine (pyrimidine and thiazole) are supplied to it separately, but *Neurospora crassa* requires only thiazole and can therefore synthesize pyrimidine for itself. The parabiosis of the yeast *Rhodotorula rubra* with the phycomycete *Mucor ramannianus* also deserves attention. The former is thiazole autotrophic and requires only pyrimidine, while the latter synthesizes pyrimidine but requires thiazole. When both organisms are inoculated onto a thiamine-free nutrient medium they thrive well when present together, but neither of them grows in the absence of the other.



Thiamine



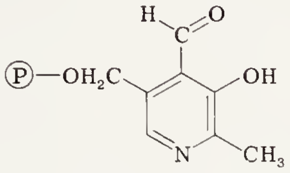
Riboflavine

Riboflavine (Vitamin B_2, Lactoflavine)

Riboflavine which has already been mentioned as a component of the flavine enzymes, is required by *Lactobacillus casei* as a growth factor.

Pyridoxal (Vitamin B_6)

Pyridoxal and its derivatives (pyridoxine, pyridoxamine) are precursors of pyridoxal phosphate (see p. 241) of the coenzyme of amino acid decarboxylases and transaminases. The needs of the various microorganisms with respect to this vitamin vary to some extent. Many *Lactobacillus* species require pyridoxal phosphate itself, while others can make do with precursors.



Pyridoxal
phosphate

Pantothenic Acid

A component of coenzyme A, pantothenic acid acts as a growth factor for many yeasts and for some *Lactobacillus* species.

Nicotinic Acid

Nicotinic acid or nicotinamide, is a constituent of the often mentioned nicotinamide adenine dinucleotide; it is a growth factor for lactic acid bacteria.

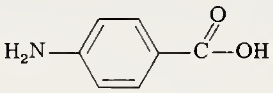
Apart from the microorganisms just mentioned, which are normally incapable of synthesizing the respective growth factors, such studies have often been carried out using nutrient deficient mutants (see p. 310) obtained by irradiation of wild forms which are independent of the respective substance.

ANTIMETABOLITES

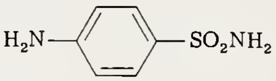
The dependence of microorganisms on specific growth factors affords the possibility of inhibiting their development in a specific manner by supplying substances which are to some extent similar to the respective growth factors and are taken up by the microorganism instead, but which cannot replace the original growth factor functionally. This results in certain deficiency symptoms and in the slowing down or cessation of growth. Such substances are known as antimetabolites.

Sulfonamides

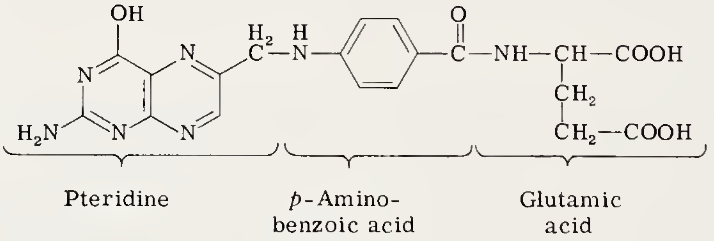
The classic examples of antimetabolites are the sulfonamides, whose action was discovered by Domagk[1] in 1932. As is now well known, sulfonamides (an example of which is sulfanilamide) act as antagonists of *p*-aminobenzoic acid (PAB, vitamin H′), which is a component of folic acid; the latter is a growth factor essential for many microorganisms. Folic acid, in turn, is the active group of coenzyme F, which transfers C-1 groups (transformylation). In view of the similarity of their molecular structure, the sulfonamides, when offered to microorganisms in large quantities, are built into folic acid to the exclusion of PAB; the folic acid is thereby deactivated. This stops the growth of the microorganisms, although it does not kill them. If PAB is now given in excess, it displaces the sulfonamides and growth starts again.



p-Amino-
benzoic acid



Sulfanilamide



Folic acid

By a systematic examination of a large number of compounds, the number of known antimetabolics has increased greatly in recent years. Thus, for example, pantothenic acid hydrazide acts as the antimetabolite of pantothenic acid, and Isoniazid, a drug used to control tuberculosis, acts as an antimetabolite of pyridoxine (see above). Many of these antimetabolites have found application as drugs in medicine along with the sulfonamides. Moreover, they are invaluable to biochemists and biologists, since they can be used to block certain specific physiological processes; this makes the study of such processes much easier or even at all possible.

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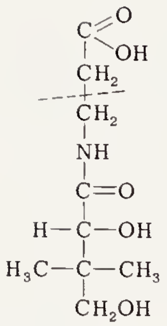
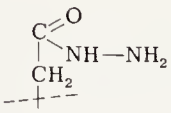
[1] Domagk was awarded the 1939 Nobel prize for medicine for his work in the field of sulfonamides.



Pantothenic acid



Pantothenic acid hydrazide

ANTIBIOTICS

Another group of growth inhibitors are the antibiotics. As far as is known, the action of these compounds too is based on the blocking of certain metabolic processes and is therefore fundamentally similar to that of antimetabolites, but they have been given a specific name since they are produced by certain microorganisms and are secreted by them into the environment. Antibiotics inhibit the development of other microorganisms while they are harmless within wide concentration limits for the organism producing them. They can therefore be regarded as the means which allow the organism to maintain itself in a natural environment against the rest of the microflora. Similar substances are however produced by other plant groups, which are not microorganisms, among others by higher plants, so that the original definition is now hardly tenable. Chemically these substances are of various kinds, and they interfere with metabolism at specific stages; what these stages are is still often obscure.

Penicillin

Penicillin was discovered by Fleming[2] in 1929 and its structure was elucidated by Chain, Florey, and their co-workers in 1941; it was the first antibiotic to be discovered. It is a product of the mold *Penicillium notatum* but is now obtained in practice mostly from *Penicillium chrysogenum*. It is, however, synthesized by other fungi as well. A number of penicillins, which differ only slightly in their structure, are now known and these are designated by capital letters (B, F, G, etc.).

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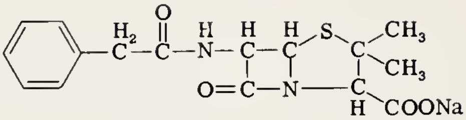
[2] Sir Alexander Fleming was awarded the Nobel prize for medicine in 1945 for this work.



Penicillin G-Na

Penicillins inhibit especially the growth of gram-positive bacteria, e.g., that of staphylococci (*Micrococcus pyogenes* var. *aureus* and others). Their action seems to depend mainly on the fact that they block the synthesis of murein (muramic acid) (see p. 107) by preventing the formation of cross-links between muropeptide molecules through the peptide side-chains. In this way it is possible to produce certain bacterial species as protoplasts without cell walls. The resulting forms are often of abnormal shape and are overgrown; they are also known as "large bodies." Penicillin remains to this day the most frequently used antibiotic, though in recent times, the occurrence of penicillin-resistant strains has been noted with increasing frequency. In some cases this resistance is caused by the formation of the enzyme penicillinase which decomposes penicillin.

The discovery of penicillin started an intensive search for further antibiotics in recent decades. In the course of this search, tens of thousands of strains of various microorganisms were tested for antibiotie activity, and several hundred active substances were discovered in this way. Many of these have, however, been proved identical to ones already known, and many others were found to be toxic to humans and animals, so that only a few have found application in medicine.

Several experimental methods have been used to test for antibiotic activity, although in thc final analysis all depend on the same principles. The fungus to be studied is grown in an artificial medium and, after a period of time, the culture filtrate is tested for its antibiotic activity. This can be done, for example, by the well test (Fig. 16.2). In this test,

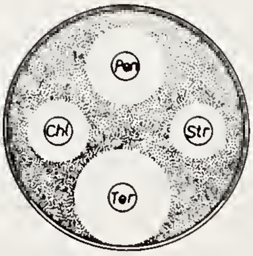
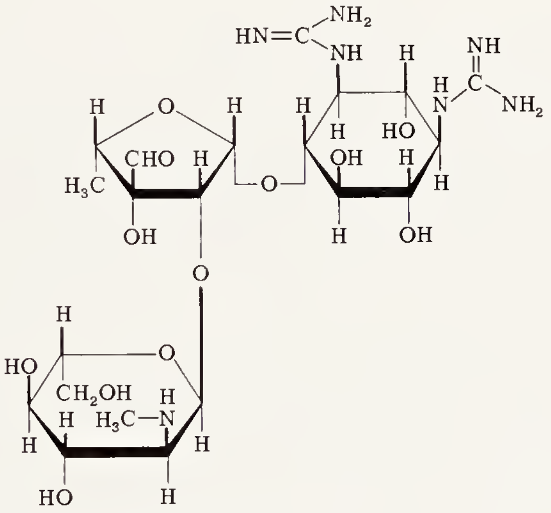


FIG. 16.2. Comparison of the action of antibiotics: penicillin (Pen), streptomycin (Str), Terramycin (Ter), and chloramphenicol (Chl) acting on *Micrococcus pyogenes* var. *aureus* in the well test.

the nutrient agar plate is first inoculated with the bacterium under investigation. Wells are then punched into the plate and are filled with the culture filtrate that may contain an antibiotic. After a suitable interval the region of the wells is inspected to see whether bacterial growth has been inhibited. Basically, the organism to be tested for antibiotic activity could itself be inoculated onto the test plate and the perimeter of its colonies could be investigated for zones of inhibition. This is how Fleming discovered antibiotic activity in a bacterial culture contaminated accidentally with *Penicillium notatum*. Only a few of the antibiotics now used in medicine can be mentioned here.

Streptomycin

Produced by the actinomycete *Streptomyces griseus*, streptomycin has a broader spectrum of action than penicillin, i.e., it inhibits the growth of a greater number of bacterial species. It is used widely in medicine alongside penicillin, but its mode of action is as yet very obscure.



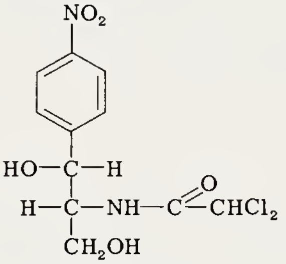
Streptomycin

Chloramphenicol

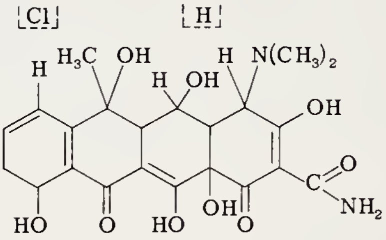
Chloramphenicol (chloromycetin) is also a product of an actinomycete, *Streptomyces venezuelae*, and is now produced synthetically. Its molecule is interesting in that it contains a nitro group, which is rare in natural products. It is active against numerous gram-positive and gram-negative bacteria and against many protozoa and large viruses. Its action seems to depend on inactivation of RNA and the resulting blockage of protein synthesis.

Aureomycin and Terramycin

Two other *Streptomyces* products, Aureomycin and Terramycin are closely related derivatives of tetracycline, the molecule of which consists of four condensed ring systems. Their spectrum of action is broad, like that of chloramphenicol.



Chloramphenicol



Terramycin
(Aureomycin)

Growth of the Higher Plants

Specialization of the functions of cells and tissues in a multicellular organism, which increases in higher plants, requires a further morphological and physiological transformation of the cells produced in the meristems by division. This transformation consists partly of an increase in the cell size by longitudinal, apical, and lateral growth, and partly of a number of processes which lead to the development of the final cell shape and which have been described in Chapter 4 by the collective term "differentiation." The following processes can be mentioned in this context: the growth in thickness of the cell wall; incrustation and accretion; formation of certain plasma structures; and formation of special cell materials.

Three phases of cell growth are normally distinguished: cell division; cell enlargement; and cell enlargement (vacuolation) associated with differentiation. Cells undergo these phases in succession. In the case of root tips this occurs approximately simultaneously in cells of similar age. It therefore follows that three growth zones are found here, which are correspondingly called meristematic, elongational, and differentiation zones (Figs. 8.1 and 16.3). These zones are, of course, not sharply defined but rather overlap (see p. 170).

The three classic growth zones in roots reported above are quite different from the pattern of growth seen in a developmental study of

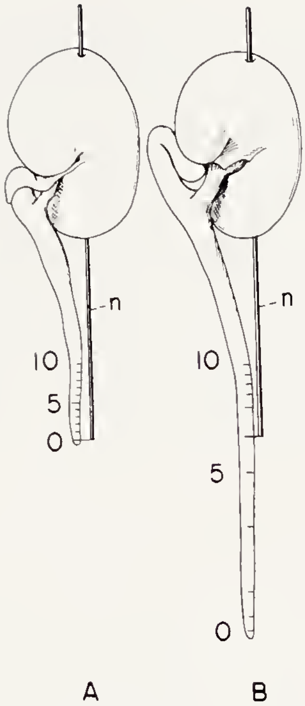


FIG. 16.3. Distribution of the growth increment at the root tips of broad beans (*Vicia faba*). (A) Root tip divided into 10 equal intervals with India ink. (B) The same root 22 hours later. The marks are displaced from each other to various extents by the uneven elongational growth of the individual zones. The three zones lie approximately between the marks as follows: 0–2, cell division zone; 2–7, elongation zone; over 7, differentiation zone. The needle (*n*) marks the original position of the zero point. (After Sachs.)

the root. Jensen (1958) showed that cellular growth in onion roots is divided into three phases. The first phase, limited to the distal 1 mm of the root is made up entirely of radial expansion; the second or transition phase (1.0–1.5 mm back from the tip) is characterized by both radial expansion and cell elongation; the third phase from 1.5 mm to approximately 1 cm back from the tip is characterized by the cessation of radial expansion but rapid cell elongation. Differentiation then begins with the formation of root hairs, the differentiation of the endodermis, and then the vascularization of the central cylinder.

In the growing points of stems no such division into growth zones is usually made (see p. 129), but it could be. Cell division extends to the base of the pith rib meristem (Fig. 6.1B). Cell elongation is obvious in the files of cells in the presumptive pith and cortex. In a recent developmental study of the shoot tip (West and Gunckel, 1968) three growth phases were noted and compared with Jensen's (1958) work on the root. The first or initial growth phase occurs in the distal 0.5 mm of the shoot and is characterized by very rapid cellular growth, including both radial expansion and cell elongation. In the second phase (0.5 mm to 4–5 cm) radial expansion continues, but cell elongation abruptly ceases at 0.5 mm. In the third growth phase, more than 4–5 cm back from the shoot tip, rapid cell elongation resumes. Hence, in terms of direction, cellular growth in the two systems, root and shoot, is dissimilar.

Cells produced by the cambium (cf. Figs. 6.1C and 6.9) and by other meristems will, of course, also undergo corresponding development. The same holds for other intermediates between the unicellular and multicellular types which have been discussed in Chapter 5 insofar as their cells exhibit a subdivision of functions.

CELL DIVISION AND PLASMA GROWTH

In higher plants cell division occurs mostly in the meristematic sections of the growing points (cf. Fig. 5.19) and also in the other primary and secondary meristem tissues. It has, however, already been indicated (see p. 147) that this restriction is not an absolute one, as cell divisions may also occur extensively below the stem growing point with elongation of internodes. In grasses (cf. Fig. 6.14) there are even special intercalary growth zones which remain active for long periods of time.

As has already been discussed in the section on mitosis, each nuclear division is preceded by identical reproduction of the DNA, and each cell division is preceded by growth of plasma associated with a certain, even though limited, increase in cell size. The growth of the plasma consists first of all of a synthesis of species-specific proteins; the control of this process by nuclear DNA has already been described (see p. 312). The nucleus also controls the synthesis of other (nonprotein) materials, such as the growth factors, through the synthesis of corresponding enzyme proteins.

The way in which cell divisions are triggered off or inhibited is as yet rather obscure. The statement just made, namely that cell divisions are normally limited to certain regions of the plant body, suggests that cell divisions are also controlled in some manner that must surely also have a material basis. Thus, for example, there could be certain hormone-type materials inducing cell division in the meristem tissues which are absent from the other tissues; looking at the situation from another point of view, the cell divisions could be suppressed in the nondividing tissues by certain inhibitor substances.

In recent years, many substances capable of inducing cell divisions have actually been found. Thus kinetin (see p. 346) in association with auxin (see p. 343) can induce cell divisions in isolated medullar tissues from tobacco shoots. The primary action of kinetin, a purine derivative, seems to be to increase the rate of RNA synthesis, which results in a greater intensity of protein synthesis. An increase in cell division activity caused by other chemically as yet unidentified substances has also been observed; such substances have, for instance, been isolated from apples and tomatoes. Finally, gibberellins (see p. 345) can increase significantly the cell division activity in the subapical region of the shoot axis, while they seem to have no effect on cell divisions in the meristematic apical region.

It may therefore be assumed that cell division processes too are governed by phytohormones (see p. 343) in plants; this does not mean that the same compounds would be acting by means of which cell divisions can be induced artificially (see above). The existence of mitosis-inhibiting substances comparable to the mitosis toxins (see p. 309) in organisms, and the participation of such compounds in the control of cell division processes are still uncertain. Some phytohormones are capable of decreasing the cell division activity significantly when present in higher concentrations, so that whether they stimulate or inhibit the process may simply depend on the concentrations present in the tissues at any one time.

ELONGATIONAL GROWTH

This is the externally most striking phase of plant growth. The positions of the elongation zones in the stem and the root can be observed from Figs. 519 and 16.3. As has already been mentioned (see p. 81), cell elongation is due to growth in the surface and girth of the cell in a preferred direction. The associated increase in cell volume is accompanied by the uptake of large quantities of water (see Fig. 4.1), leading to the formation of vacuoles, while the formation of plasma substance occurs only to a limited extent that is small compared with the increase in volume.

The mechanism of elongational growth is still rather obscure. On the basis of the osmotic laws discussed earlier (see pp. 81–82) the course of the elongational growth may be as follows. The cell wall becomes plastic (unknown auxin mechanism) and the cell wall pressure decreases (auxin effect on water uptake). According to the osmotic equation of state $S_{sc} = S_i - W$, S_{sc} must increase accordingly. Water therefore enters the cell, its volume increases and the cell wall is stretched further. In reality the conditions may well be much more complicated. Since the cell wall does not become thinner on expansion (see p. 179), the elongational growth must be accompanied by the production of fresh wall material.

There is no doubt that the cell wall undergoes plastic deformation (extension) during the growth of its area. Whether the growth is assumed to be of the multiple network or of the intussusception type (see p. 82), the mesh widening of the fibrillar network must occur by one of two processes: Either the points of attachment between the fibrils are broken and reformed at other points or the individual sections of the polysaccharide molecules increase in length by the incorporation of new units into the molecular chains. Which of the two processes is actually operative is not known.

The elongational growth of the cell is governed by phytohormones. Auxin (see p. 343) seems to play a dominant role; it can be identified in a large number of plants. In line with our imperfect understanding of the mechanism of elongational growth, the mode of the action of auxins is not yet clear. According to one view, the Ca ions are leached out of the cell wall whereby the Ca bridges are broken; this would result in a loosening of the fibrillar network of the cell wall. According to another hypothesis, auxin accelerates the synthesis of fresh cell wall material. It is certain, however, that auxin increases the plasticity of the cell wall. The elongational growth seems to be affected by other phytohormones as well, as has been confirmed for gibberellins which sometimes enhance the action of auxins though they may also inhibit them.

DIFFERENTIATION GROWTH

It has been mentioned earlier that the differentiation processes begin in the stage of elongational growth; the future shape of the cell is already decided at that stage. However, these processes continue after the final cell size has been reached, and terminate only when the cell is fully equipped to carry out its future functions.

In the course of differentiation, only a limited portion of the total genetic potential of a cell is being realized, a portion that varies qualitatively and quantitatively according to the type of the cell. The genetic information, stored in the DNA molecules of the chromosomes as various nucleotide sequences, is transferred from the nucleus to the plasma by messenger RNA and is there translated into the amino acid sequence of the enzyme proteins synthesized in the manner already described (see p. 312). Corresponding to the great variety of differentiation characteristics, the differentiation process of each cell consists of many biochemical reactions and reaction chains. Each reaction step is normally governed by an enzyme, and the synthesis of a very large number of enzymes must be initiated by the formation of an equally large number of messenger RNA molecules. The problem is not just that of the synthesis of each of these enzymes; the differentiation processes can take their proper course only if the required enzymes are available at the right time and in the required sequence. This again presupposes a strong coordination of messenger RNA. The essential problem of the differentiation process is therefore the question how the cell uses a particular part of the genetic potential at any one time, i.e., which of the many possible types of messenger RNA molecules should be synthesized at a given instant.

The fact that different genes are active, i.e., build messenger RNA in different phases of the developmental process, can be observed even microscopically using suitable objects, i.e., giant chromosomes (see p. 59). The gene activity here produces the so-called puffs, circular ridges of the corresponding chromosome sections caused by the loosening and lateral protrusion of the chromonemata (Fig. 3.10E). The puffs have been shown to be sites of RNA synthesis and, therefore, active states of the chromosomes by the incorporation of isotopically labeled uridine (see p. 19). In the subsequent stages of development the puffs appear at various parts of the chromosomes and disappear after a certain interval. They are therefore active only for a limited time. There is reason to believe that the process that can be followed visually in the giant chromosomes occurs also in chromosomes of normal size.

In order to explain the activity of genes which is restricted to a certain stage of the developmental process, to certain regions of organs, and often to a certain time interval, some rather detailed though as yet rather hypothetical ideas have been put forward in recent years. These will be briefly outlined in the following section. However, like those on the transfer of genetic information (see p. 311), these ideas are largely based on investigations using microorganisms and some animal species, and it is therefore by no means certain whether they can be directly applied to higher plants, although there are indications that this may be so.

It has been shown by a series of experiments that two types of genes, blocked and exposed ones, may be distinguished. The former are blocked by the binding of histone–proteins on the phosphate groups of DNA (see p. 60) and therefore cannot become active, i.e., cannot form messenger RNA, while the exposed genes are free from histones and are at least potentially active. If the histone molecule is released from the DNA of the blocked gene or if it is replaced by a protein that does not hinder RNA synthesis, the blocked gene becomes potentially active. It is therefore reasonable to assume that the differential blocking and activation of genes produces a specific group of enzymes for the cell. These enzymes catalyse only certain reactions according to their specificity; the whole set of these reactions, when coordinated in time, leads to the development of the appropriate differentiation characteristics.

The relative quantities of individual enzymes, which is also known as the "enzyme pattern" of the cell, now do not appear invariable but rather seem to vary within certain limits. As has already been indicated, not all the exposed (i.e., potentially active) genes are actually active all the time. The cell must therefore possess further means of regulating the gene activity.

One such possibility is afforded by the regulator–operator hypothesis, based on recent investigations concerning enzyme induction (enzymic adaptation) in microorganisms.[3] According to this view, the activity of structural genes, which determine the structure of the enzyme proteins to be built, is controlled by operator genes. One of the latter, together with one or more structure genes, forms an operative unit called the operon. The operator gene is in turn under the control of a regulator gene, which blocks the operator gene by producing a repressor and thereby inhibits the functions of the operon.

In the so-called *inducible systems* (Fig. 16.4A) the repressor R_1 built by the regulator gene RG_1, enters into a labile complex $[R_1S_1]$ by reaction with an inducer. In the present example this is the substrate S_1. The repressor is thus inactivated. As the operator gene OG_1 is no longer repressed by R_1 for which it normally has great affinity the structural genes of the corresponding operon, SG_1, SG_2, can become active and cause the formation of enzymes E_1 and E_2, through the corresponding messenger RNA (m_1, m_2). These transform the substrates S_1 to the end product S_3 via the intermediate product S_2. With decreasing substrate concentration the complex $[R_1S_1]$ dissociates increasingly into its components, so that the operator gene OG_1 is finally repressed again by $R_1 = R'_1$ and suppresses the activity of the operon.

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[3] F. Jacob and J. Monod together with A. Lwoff shared the 1965 Nobel prize for medicine for their work in the field of gene regulation which finally led to the regulator–operator hypothesis.

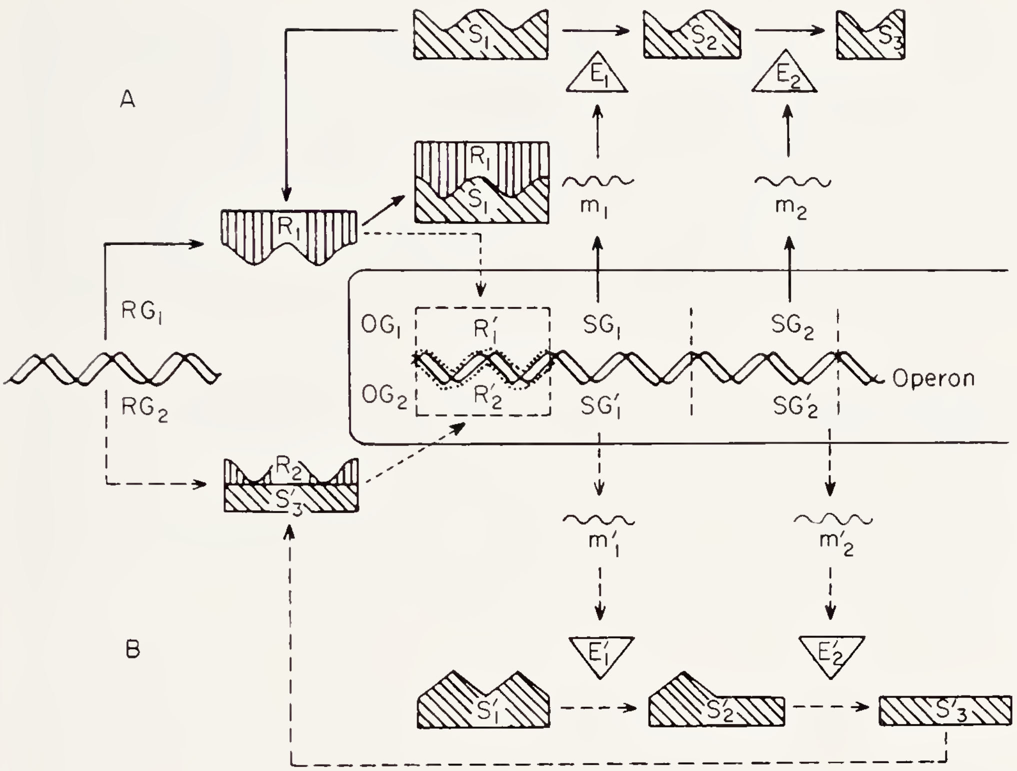


FIG. 16.4. Schematic regulation of gene activity. (A) Inducible system; (B) repressible system. RG, Regulator gene; R, repressor; OG, operator gene, SG, structure genes; m, messenger RNA; E, enzymes, S_1, substrates, S_2, intermediate products; S_3, end products.

In *repressible systems* (Fig. 16.4B) the so-called aporepressor R_2 is first activated by the end product S'_3 of the respective enzyme reaction, which acts as a corepressor. With increasing concentration of S'_3, R_2 and S'_3 combine to form the active repressor R'_2. This represses the operator gene OG_2 and hence blocks the activity of the structure genes SG'_1 and SG'_2 of the operon.

The above hypothesis could explain many of the open questions and provide valuable insight into the differentiation phenomena; but the small number of operons identified in higher forms may make application of the Jacob-Monod model difficult. Also, it is as yet rather unclear, for example, how external factors can affect this control system and how they trigger a differentiation process (see p. 356). For example, the availability of substrates and cofactors and energy levels may limit protein synthesis. In addition to genetic repression the other intercellular control mechanism is *feedback inhibition*—inhibition of an enzyme by a distant product of its activity. Additionally Mintz presented evidence (see Bernhard, 1969) that competition and selection among variant embryonic clones may play a role in development. Also cell aging reduces the developmental potential of cells. Gross morphological changes that result in adult animal shape are affected by a combination of differential cell growth and the programmed death of large numbers of imaginal disc cells (Saunders and Fallon, 1966). In summary, the one-gene–one-enzyme concept of genetics is no longer tenable. There is much more variability in products of a single gene than we had previously thought and many more modifying factors. The chemical nature of the inductors and repressors in higher plants is also virtually unknown. It is known that many phytohormones (see below) are able to accelerate the course of certain differentiation processes, but this is undoubtedly a nonspecific acceleration effect and not a specific one bringing about certain differentiation processes. The great variety of differentiation processes can hardly be expected to be controlled by a relatively small number of phytohormones. Or can they? See p. 347.

Control of Organ Development

A plant organ consists of many cells which are differentiated to various extents. Depending on the structure of the organ in question, the arrangement of these cells corresponds to a strictly defined pattern, the so-called differentiation pattern. It is therefore obvious that organ development must involve a much greater number of differentiation processes than the development of a single cell; moreover, the course of these processes in individual cells must be coordinated according to the differentiation pattern. Our present knowledge concerning the differentiation processes in cells is rather limited, and this applies to a still greater extent to the ideas about organ development, where even the basic phenomena cannot be interpreted satisfactorily. Such basic phenomena of organ development are (among others) polarity, cell determination, and correlations.

POLARITY

Polarity is the physiological nonequivalence of opposite regions of individual cells or of whole organs, often expressed in morphological differences between the two poles. Such nonequivalence may occur even at the lowest levels of organization. Thus, for example, two poles (one of them light sensitive and provided with a flagellum and the other insensitive to light and without a flagellum) develop in the purple bacteria, *Thiospirillum jenense,* and also in flagellates (see p. 111). In *Volvox* (see Fig. 5.8A) one of the poles is vegetative and the other generative; in many thalli the polarity develops between a dividing apical cell and a basal rhizoid cell. The most striking example is, however, the development of the stem and root poles in higher plants, which is apparent already in the first phase of embryonic development (see p. 282).

The polarity can often be observed even in single cells of an organ. It manifests itself, among others, in the one-way (i.e., polar) transport of certain materials and also in the impossibility of grafting cells taken from a tissue back onto the same organ with a reversed orientation, although the grafting is easily accomplished when the cells are inserted into the tissue with their original orientation. This is why grafts on trees and shrubs succeed usually only when the apical pole of the grafting base is connected to the basal pole of the graft. The molecular and structural causes of polarity are still unclear, but it appears that the carriers of polarity, e.g., auxins, are mainly found in the cell walls or the peripheral layers of the protoplasts. This is supported by the observation that polarity remains in existence even in cells featuring strong plasma currents (see p. 75).

The induction of polarity occurs in unpolarized or weakly polarized cells, e.g., the meiospores of mosses and ferns, and also in the fertilized oospheres of many algae (*Fucus*), in the first phase of development; it therefore precedes the first cell division. In the examples just mentioned the polarity can be induced by external factors such as light or gravity. In the first mentioned case the first unequal division gives rise to the smaller, lens-shaped, rhizoid cell on the darker side, i.e., on the side that is normally turned away from the light (Fig. 16.5A,B). In the case of gravity induction it is formed on the opposite side. The rhizoid cell then grows into a more or less colorless rhizoid, while the prothallium develops from the remaining part of the cell by several cell divisions (Fig. 16.5C). Polarization does, however, eventually occur even if all inducing factors are carefully excluded; it has presumably an autonomous character. Basically, all cells produced by division from a polarized cell exhibit the same polarization as the parent cell.

Once the polarity has been induced, it is normally permanently preserved both by individual cells and by the whole organ. This is proved conclusively, apart from the grafting experiments just mentioned, by the classic willow shoot experiment.

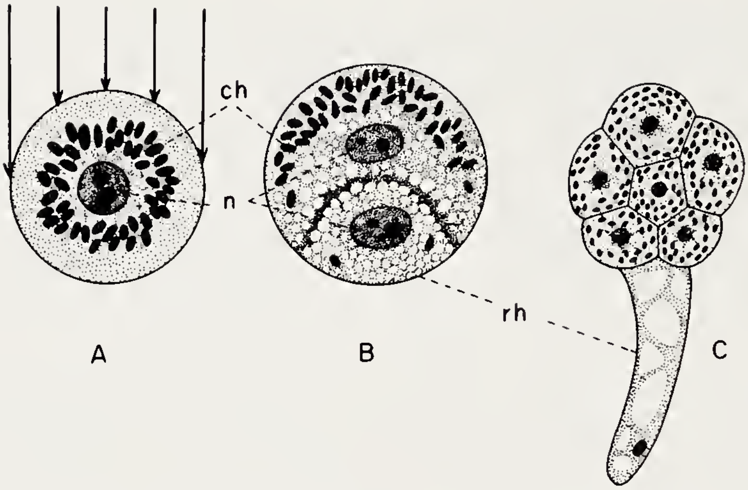


FIG. 16.5. Induction of polarization in a spore of horsetail (*Equisetum*) by light. The direction of illumination is shown by arrows. (A) Illumination of the still unpolarized spore; (B) segregation of the lens-shaped rhizoid cell at the dark pole; (C) later stage with rhizoid and multicellular prothallium. ch, Chloroplasts; n, nucleus; rh, rhizoid cell. (After Sadebeck.)

A willow shoot is subdivided and the parts are suspended in a moist place so that one of them retains its original orientation (Fig. 16.6A) while the other is suspended upside down (Fig. 16.6B). The side shoots and the roots appear at the original upper and lower ends, respectively, irrespective of the actual orientation of the suspended shoots. This behavior is determined by the one-way transport of phytohormones (see p. 343) in the phloem toward the base caused by the polarity gradient. If this transport is interrupted by cutting away a section of the phloem (bark) on the shoot (Fig. 16.6C) then, physiologically, two individual pieces are produced, both of which develop side shoots at their upper ends and adventitious roots at the lower.

DETERMINATION AND DIFFERENTIATION

Determination is a process in which part of the genetic information stored in the embryonic cell is selected for realization in the differentiation process. Each embryonic cell in any one organism contains the same genetic information and therefore the same potential for development; the agencics of the determination can thus hardly be expected to be contained in it as well.

One of the factors of determination, which has already been discussed, is polarity. Each cell division occurring in a direction perpendicular to

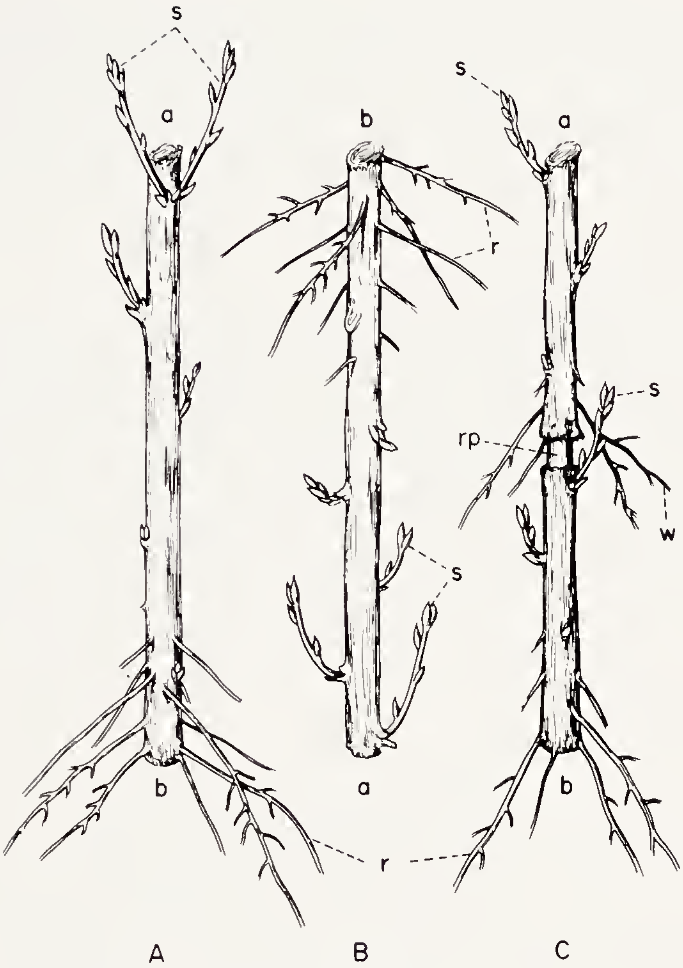


Fig. 16.6. Polarity of emerging willow shoots (*Salix*): (A) Normal position; (B) inverted position; (C) normal position, with a section of the phloem (bark) cut away. a, Apical; b, basal pole; rp, ring phloem removed here; s, side shoots; r, roots. (After Sachs and Pfeffer.)

the polarity gradient must produce two physiologically nonequivalent daughter cells. Another factor may be the concentration gradient of various materials in the tissues. Thus, for example, the differentiation of the outermost tunica layer to form the epidermis may well be determined by its contact with the surrounding atmosphere. The decisive factor here may be either the moisture gradient, which decreases from the inside to the outside of the organ, or the concentration gradients of oxygen or CO_2. A complicated interaction of these factors is probably involved. These radially oriented gradients could, of course, also be significant for the deeper cell layers. The individual differentiation processes may therefore be regarded as see-saw processes; such processes take place in a certain direction in the presence of a given concentration region of the controlling agent, and in a different direction if the concentration of the controlling agent exceeds or fails to reach certain limiting values. Salts or their ions could also be of importance. Thus, the development of the mesophyll of foliage leaves depends markedly on the $K^+:Ca^{2+}$ ratio. Finally, concentration and energy gradients resulting from a variation in the metabolic activity of certain cells and tissues could also be decisive.

The latter possibility leads to the development of differentiation patterns due to an inhibiting effect. An inhibition effect is exhibited by a cell differentiated in a certain manner when it inhibits similar differentiation processes in its immediate neighborhood. Thus, for example, (see Fig. 16.7) the stomate initials formed during differentiation of the epidermis in hedge garlic inhibit the formation of further stomata until, as a result of the increase in epidermis area, they become so far removed from each other that the inhibition effect can no longer operate. Fresh initials are then formed in the gaps produced between the inhibition zones.

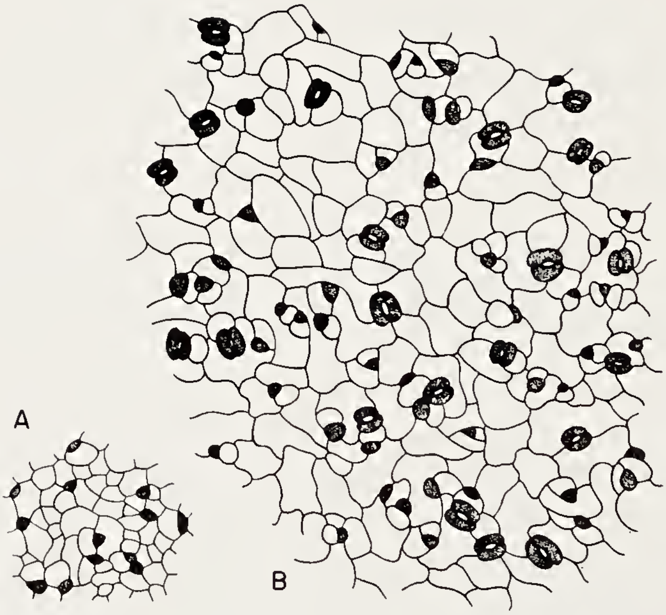


FIG. 16.7. The epidermis of *Alliaria officinalis* (hedge garlic). (A) Very young leaf, on which stomate initials are formed at certain intervals after the termination of the embryonic cell division activity. (B) Older leaf. Here the original stomata have become so far removed from each other due to the increase in leaf area that the inhibition zones are no longer everywhere in contact. Fresh initials are formed in the gaps thus produced. [After Bünning and Sagromsky (1948).]

Apart from the factors just mentioned, many others, some of them probably still unknown, may affect the development of the differentiation pattern. The few examples just given were only designed to illustrate the complicated manner in which internal and external factors interact in the differentiation process.

CORRELATIONS–PHYTOHORMONES

In addition to the above, there are certain interactions (correlations) between neighboring organs and between organs which are located at some distance from one another. One instructive example of this is apical dominance, which occurs in many plants. Apical dominance is the suppression of side shoots on a stem axis by the apical growing point. If the latter is removed by decapitation, the auxillary bud immediately below will emerge. This raises the question of how this action is exerted at a distance.

A close study of the interrelations of various organs has shown that certain substances exhibiting hormone character, i.e., the growth substances or phytohormones, play a decisive part in the correlative control of organ development in plants. It appears that the plant organism, like man and other animals, contains an internally balanced hormone system, the components of which can influence one another antagonistically or synergistically. The question whether or not a certain developmental process is initiated independently depends not only on the absolute hormone concentration in the tissue region in question, but also on the ratio of the quantities of the various hormones. The chemical compositions and actions of some of these hormones are already known in considerable detail, but it must be assumed that a number of other phytohormones, whose nature are not yet known, also carry on their functions in the living organism.

Auxin

Auxin (indole-3-acetic acid, IAA) is already familiar to us as an elongation hormone (see p. 334). However, it also has many other functions. Thus it is probably also responsible for the apical dominance mentioned earlier. If a hormone paste containing IAA is spread on the tip of the decapitated shoot, the growth of side shoots is again suppressed. A constant stream of hormone evidently flows downward from the apical meristem and young leaves and somehow plays a decisive part in the inhibition of bud or side shoot growth. Root formation *on cuttings,* on the other hand, is strongly promoted by IAA. In the *intact* plant, however, auxin along with RNA promotes growth in stem length along a polarized axis in high concentrations, inhibits buds at intermediate concentrations, and favors root growth at low concentrations (Fig. 16.8). Auxin initiates growth and active protein synthesis in dividing cells but the synthesis is highly aberrant (producing large amounts of proline). Some other effects of IAA will be mentioned later.

Skoog and Tsui (1951) did some experiments on the chemical induction of organs on pith parenchyma and *excised* stem segments of tobacco. Auxin tended to stimulate rooting and to depress shoot formation at about 0.02 mg/liter. Adenine (40 mg/liter) (kinin) stimulated shoot formation and inhibited rooting. In its simplest form growth and differentiation would be simply a matter of balance of auxins and kinins. Actually, a concentration of 0.005 mg/liter of auxin and 40 mg/liter adenine produced both shoots and roots. However, these results have not been duplicated for any other explant tissues nor in intact plants.

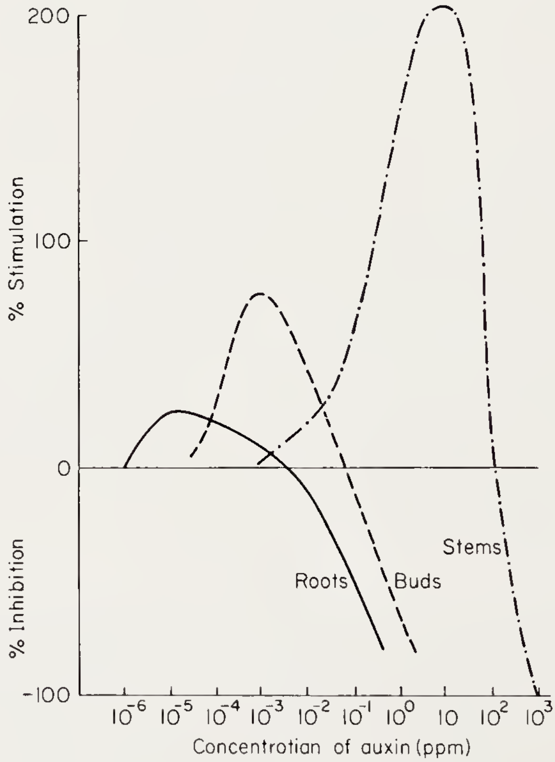
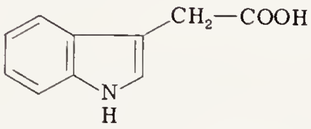


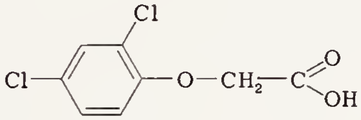
FIG. 16.8. Response of plant organs to exogenously supplied auxin. The curves do not necessarily represent the relationships between internal auxin concentrations and growth rates. Notes particularly that the optimum concentration for the growth of each plant organ differs so that, for example, the concentration of indoleacetic acid that favors stem growth is inhibitory for the growth of buds and roots. (After Thimann.)

Subsequently it was found that gibberellin prevents the formation of both organs. This brings us to the point, discussed below, that for now the control of plant growth, once initiated, does not reside with one phytohormone but with a balance of many factors.

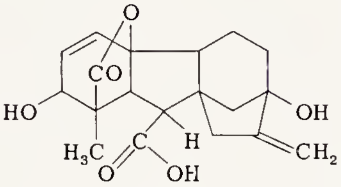


Indole-3-acetic acid

Many compounds with hormonelike characteristics have been synthesized in recent years. Some of them are indole derivatives and others are chemically quite different. The best known example is 2,4-dichlorophenoxyacetic acid. Many of these hormones act as growth inhibitors when present at higher concentrations, and they are therefore used to suppress unwanted plant growth, i.e., as herbicides.



2,4-Dichloro-phenoxyacetic acid



Gibberellic acid

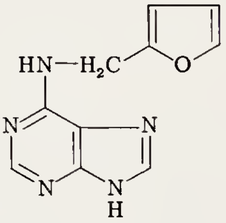
Gibberellins

These compounds have also been mentioned among the materials promoting elongation; the structural formula of gibberellin A_3 (gibberellic acid) is given above. This was first isolated from *Gibberella fujikuroi,* a fungus infecting rice plants and causing abnormal elongational growth in the infected plant. It has since been found, however, that it is widespread in higher plants too, and it apparently belongs, together with auxin, to the normal hormone complement of the plant. Gibberellins produce many other effects beyond causing elongation of intact stems and particularly of buds released from inhibition; some examples are the induction of flower development (see p. 359) and the initiation and termination of dormant states in seeds and buds. In contrast to auxin-regulated cell elongation requiring RNA, gibberellin-regulated cell elongation requires DNA synthesis. The mechanism of gibberellin action, especially at the cellular level, is still unknown.

Gibberellin alone has no effect on differentiation but when used with auxin parenchyma tissues may become differentiated into extensive xylem and phloem with a continuous cambial layer between. This differentiation effect is partly inhibited by kinetin.

Cytokinins

A third group of growth regulators are the cytokinins. The most thoroughly studied member of this group is kinetin, a 6-furfurylaminopurine. Kinetin is a product of acid hydrolysis of DNA and was first isolated from nucleic acid containing animal tissues but is commonly derived from yeast DNA. Apart from stimulating cell division, which has already been mentioned (see p. 333) it also interacts with auxin to remove bud inhibition, retards senescence or aging phenomena, controls possibly the condition and the function of cell membranes, and with auxin promotes normal protein synthesis very strongly. The primary point of entry of kinetin into these reactions and the mechanism of their action are not yet known in detail. Many experiments indicate that, in general, kinetin, activates the metabolism by furthering active transport (see p. 191), which promotes the availability of materials, and by inhibiting the removal of materials from certain tissue regions (retention). According to other evidence, kinetin could be governing protein synthesis by controlling the synthesis of RNA.



Kinetin

Many substances exhibiting similar activity have been identified in plant tissues in recent years and have been extracted. The structure of these cytokinins is mostly still unresolved.

The observation that the phytohormone concentration is not uniform throughout the tissues of a plant organism indicates that phytohormones are formed and activated in certain centers and are then transported to the sites of their utilization. Such centers of formation and activation are, e.g., the cotyledons in young plants and in older plants mainly the very young foliage leaves. The transport may occur either from cell to

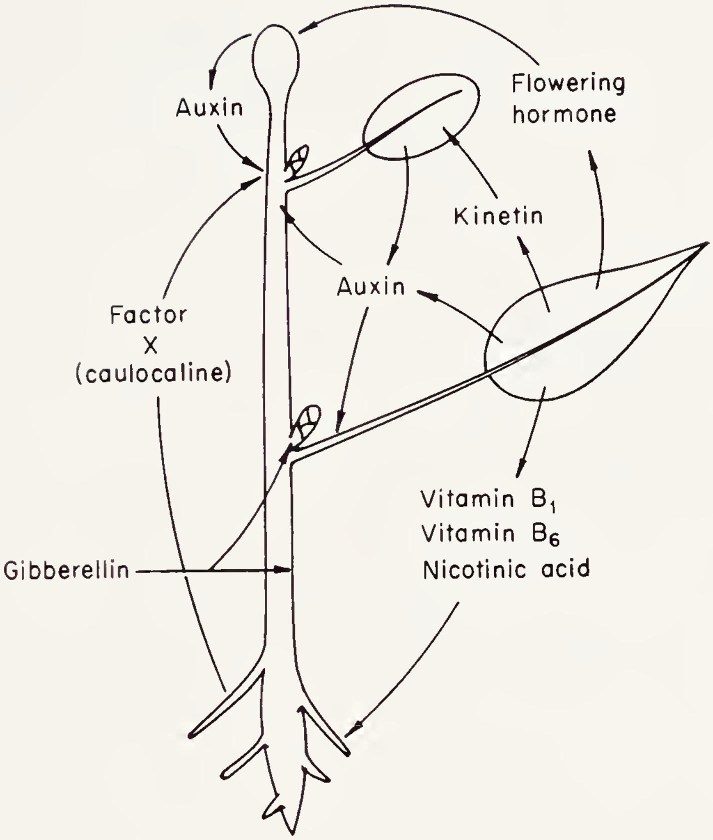


FIG. 16.9. Phytohormone growth correlations. (Modified from Went.)

cell or over longer distances, also along the sieve tubes (see p. 190). In any case, the interaction of phytohormones correlates plant growth and differentiation (see Fig. 16.9).

MORPHOGENETIC SUBSTANCES

The effect of phytohormones on organ development, described in the preceding section, does not mean that they possess specific organ-forming effects. Their primary function is on the rate of the development processes, either promoting or inhibiting them. The question then arises, whether there are any specific "organ-forming" (morphogenctic) substances beyond the ubiquitous and therefore nonspecific phytohormones. While no such substances have yet been isolated, their existence is not unlikely. This is indicated for instance by the so-called galls; these are certain excrescences caused by insects (e.g., wasps), fungi (e.g., witch's broom), bacteria (e.g., root tubercles), or other deformations of the plant organism. The galls, especially those caused by insects, are quite distinct morphologically and anatomically, depending on the species of the causal agent. This specificity necessarily depends on certain differentiation processes which do not take place in normal plants. It must therefore be assumed that specific substances are transferred from the eggs or from the emerging gall insect into the plant tissues, and that these substances induce the tissues to build galls. These materials could, of course, again be nucleic acids but at least one active substance has been identified as indoleacetic acid (Allen and Allen, 1954).

The role of inductors also applies apparently to the morphogenetic substances of the mushroom-shaped alga *Acetabularia*. The existence of these substances was revealed by grafting experiments which can be carried out as follows. In its first stage of development *Acetabularia* is unicellular and monokaryotic. The rhizoid portion, containing the nucleus, is cut off of an individual belonging to a certain species, say *A. wettsteinii*, and this cutting is grafted onto another cutting without nucleus or pileus, belonging to another species, say *A. mediterranea*. The resulting hybrid will then develop a pileus like that of *A. wettsteinii* (Fig. 16.10). Pileus development is therefore controlled by the nucleus, which emits "pileus-forming" substances into the plasma.

However, this experiment, which has provided a deeper insight into the relationship between the nucleus and the plasma and has clearly revealed the role of messenger RNA which is obviously involved in the process, cannot decide the question whether morphogenetic substances exist or not. These have been defined as substances initiating certain developmental processes, i.e., inducing first the synthesis of the required messenger RNA. They are therefore supposed to be materials acting as "inductors" according to the hypothesis outlined above (see p. 336) and to put the repressors out of action. The as yet hypothetical "flowering hormone" could be such a substance; the role of this substance will be discussed later (see p. 360).

RESTITUTIONS

It has been stated above that the differentiation processes realize only a part of the total genetic potential of the cell. However, this does not mean that the part that has not been put into effect has also been eliminated. This is shown quite clearly in cases in which already differentiated cells return to their embryonic condition after the lifting of the correlative inhibition. This can be observed, e.g., in injured plant organs, when cell divisions are resumed at the point of injury. A callus tissue

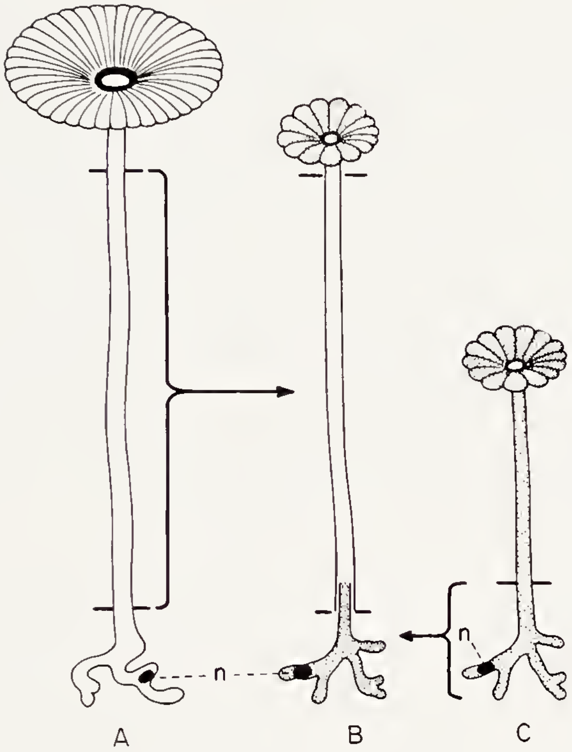


FIG. 16.10. Transplantation in *Acetabularia*. A section of the stem of *Acetabularia mediterranea* [(A), white], without a nucleus, is grafted onto a rhizoid section containing a nucleus of *Acetabularia wettsteinii* [(C), dotted]. The new pileus formed by regeneration on the stem is similar to that of *A. wettsteinii* (B); n, nucleus. [After Hämmerling (1946).]

is formed first out of dedifferentiated cells, which seals the cut. When this tissue is completed, differentiation processes set in, which regenerate the damaged or lost tissue elements and which may even regenerate the whole organ. The ability for restitution is not equally well developed in all plants. In extreme cases it is even possible to induce single cells separated from the tissue to regenerate a whole individual. The tumor-like diseases of plants are of special interest in this context, as the tumorous tissues are not subject to correlative control and even exhibit a reversal of differentiation combined with a loss of polarity.

PLANT TUMORS

In the majority of cases this is caused by a bacterium: *Agrobacterium tumefaciens*. In this respect it differs from human cancer, whose origin is still debatable; nevertheless, there are undoubtedly certain similarities between the cancerous tissues of animals and plant tumors. Such common features are the unlimited growth (and thus malignant character) of the excrescences (Fig. 16.11), the irreversibility, and the loss of normal histological structure and physilogical abilities of the tissues, due to a reversal of differentiation and loss of polarity transplantability (i.e., the possibility of transferring the tumor tissues onto healthy organs where the tumor continues to grow). It is interesting to note that once the bacteria have induced tumor formation, they are no longer necessary for its further growth. It has thus been possible, using a heat-resistant plant *Vinca rosea,* to obtain tumors free of bacteria by treatment at temperatures of 46°–47°C; these tumors developed freely and could even be transferred to healthy plants.

Tumor development in plants seems to proceed through several phases. Fresh injury of the tissues, essential for successful infection with *Agrobacterium tumefaciens,* induces the cells next to the cut to produce (just like the production of a normal callus) phytohormones, especially auxin and kinins (see p. 343), and hence initiates renewed cell divisions. However, whereas hormone production and hence also cell division stops after a time in callus cells, both processes continue unabated in the tumor cells. It appears that owing to the action of the bacteria the tumor cells have lost the ability to regulate the growth processes.

It is still not very clear how tumor induction by bacteria occurs. There is considerable evidence suggesting that the cells receive from the bacteria a substance that changes them into tumor cells. This substance is known as the tumor-inducing principle (TIP). Since division of a

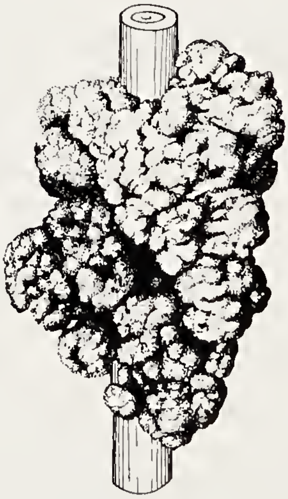


FIG. 16.11. Plant tumor on a tomato shoot, caused by *Agrobacterium tumefaciens* (approx. to scale).

completely tumorized (fully transformed) cell, even in the case of a bacteria-free tumor, always leads again to tumor cells, we must assume that the change into tumor cells is, so to speak, hereditary.

The chemical nature of TIP is naturally of great interest but, since attempts to isolate this substance have been unsuccessful so far, it is not yet possible to offer any definite statements on this point. According to recent experiments it appears to be a DNA. If this is so, the tumorization of a plant cell would be comparable to the transformation of bacteria (see p. 298). Since "foreign" nucleic acids have occasionally also been found in animal cancer cells, the modification of cells by a "wrong" nucleic acid could very well be a general tumorization principle. However, no conclusion on this point can be reached as yet because of the inadequacy of our present knowledge.

The Effect of External Factors on Development

It appears obvious that, apart from internal factors, the development of plants may be influenced by external conditions; an adequate supply of water, certain ions, CO_2, and light, essential for plant nutrition and for growth and development. In addition to these nonspecific conditions there are certain other external factors that may affect plant development quite specifically. It is thus possible for plants with similar genetic background but brought up under different environmental conditions to vary significantly in their external appearance, even though their body structure is similar. If, for example, the root system of a dandelion is divided and one half is grown at high altitude while the other half is grown at sea level, the resulting plants will be very different (Fig. 16.12). Since the mountain type assumes the appearance of the lowland form when grown in the lowlands, and vice versa, the phenomenon cannot be one of mutation. Such nonhereditary alterations produced by the environment are known as *modifications.*

RADIATION

The best investigated external factor that may influence plant development is radiation, especially radiation in the visible region of the spectrum. As has already been mentioned, in photoautotrophic organisms radiation is active, first of all, in photosynthesis. Apart from this, however, it may affect the development of the plant's external appearance in a specific manner, even in nonphotoautotrophic organisms such

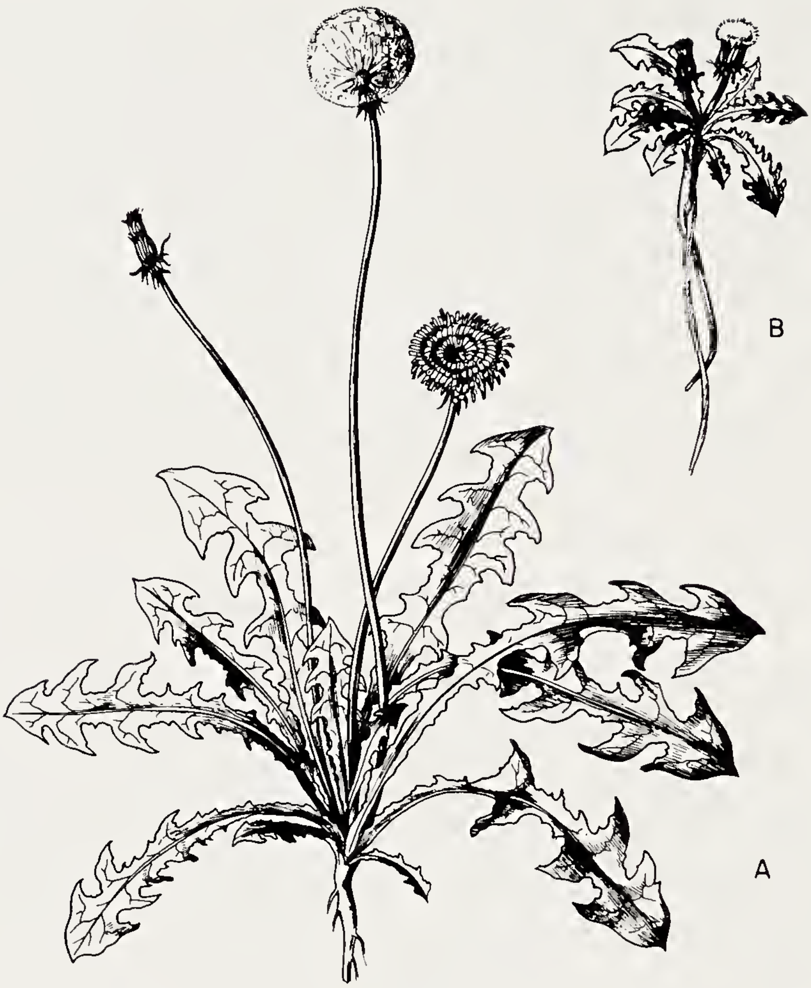


FIG. 16.12. Two individuals of dandelion (*Taraxacum officinale*) grown from a divided root system: (A) in lowlands; (B) at high altitudes. (After Bonnier.)

as fungi. This phenomenon is known as photomorphogenesis, and the effects produced by radiation are called photomorphoses.

Since the green plant is always exposed to light under natural conditions, the morphogenetic effects of radiation cannot easily be recognized. On the other hand, they are very obvious when plants grown in light are compared with those grown in the dark. This is, of course, only feasible with plants which have a sufficient supply of reserve materials and are therefore to some extent independent of photosynthesis.

The best known example is the germination of potato tubers. In light the tubers develop normal green shoots with leaves (Fig. 16.13A), while in the dark the shoots are colorless with elongated internodes and small scale-shaped leaflets (Fig. 16.13B). This behavior in the dark, known as *etiolation*, shows that light is essential for the differentiation of pro-

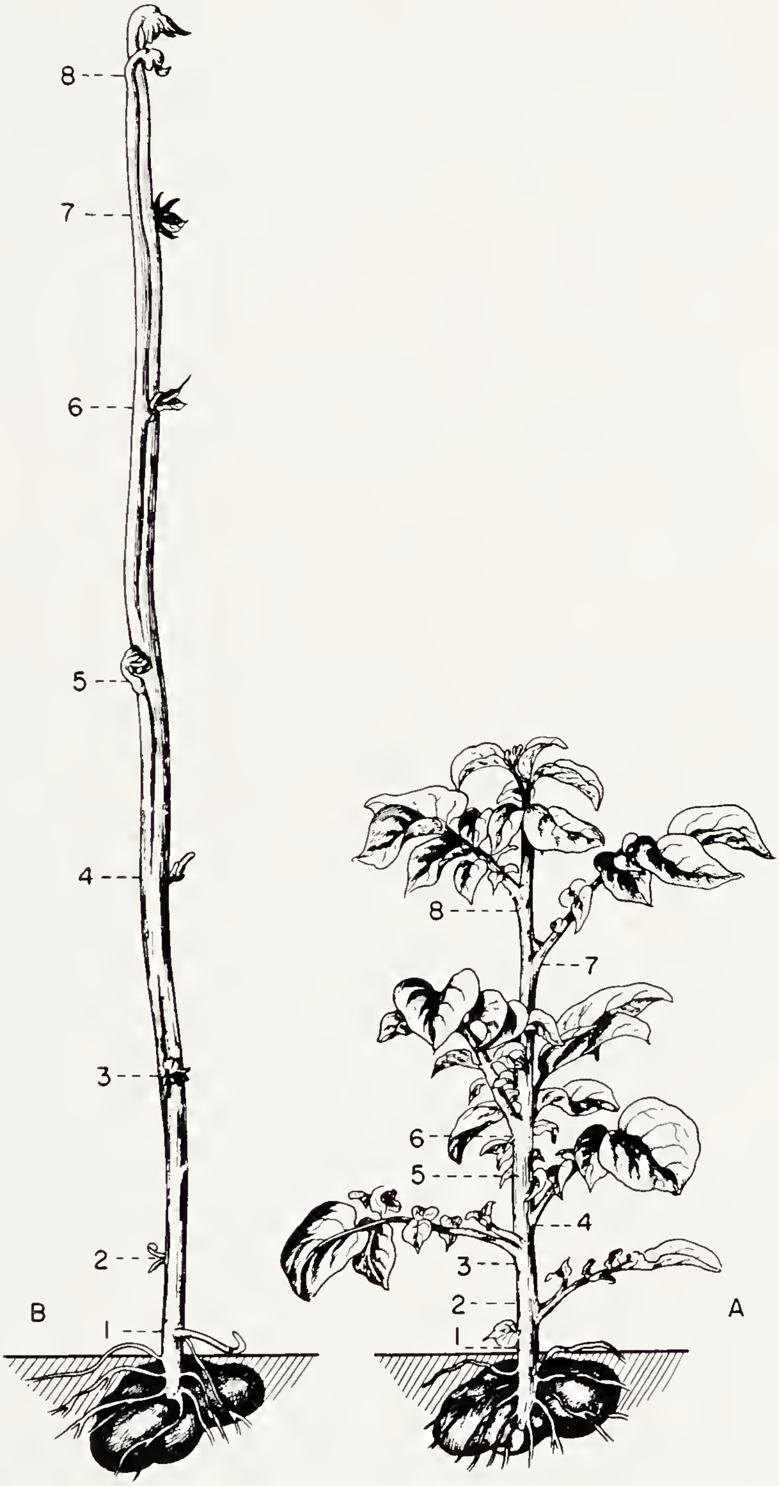


Fig. 16.13. Potato plants (A) grown in light, normal green plants with leaves; and (B) etiolated plant grown in the dark, with a pale stem and undeveloped leaves. In order to emphasize the elongation of internodes in the etiolated plant, the corresponding nodes are numbered from bottom to top. [After Pfeffer (1904, p. 98).]

plastids into chloroplasts, for the synthesis of chlorophyll, and also for the normal development of the leaf blade, while it inhibits to some extent the elongation of internodes. Since the potato tuber has a sufficient reserve of materials, and since the etiolation can be suppressed by relatively small quantities of light, negligible for photosynthesis, it can be concluded that the effects produced are specific photomorphogenetic ones.

Further effects that radiation may have on plant development include the already discussed induction of polarity (see p. 339), stimulation or inhibition of seed germination, formation of anthocyanins, effects on mitotic activity, stimulation of the formation of sporangia, and fruit bodies in fungi.

Since it has been pointed out already (see p. 205) that only absorbed radiation can be effective, the question of the pigment system absorbing the radiation arises once more. The earlier view according to which only short wavelengths (i.e., the blue region of the visible spectrum) are active, is now known to hold only for fungi. In higher plants the red region has also proved extremely active. Investigation of the action spectra[4] of various photomorphogenetic processes has shown that apparently quite different photochemical reaction systems can be responsible for photomorphogenesis.

The system studied most extensively so far is the light red-dark red system (phytochrome system) responsible for the absorption of radiation in a large number of photomorphogenetic processes. It consists of two reversibly interconvertible chromoproteins, one of which, known as P_{660}, absorbs mainly light red (near red) radiation with an activity maximum of about 660 nm, while the other known as P_{730}, absorbs essentially dark red (far red) and infrared radiation (Fig. 16.14). Absorption of light red radiation transforms P_{660}, the physiologically inactive form, into the active P_{730} form. Subsequent irradiation with dark (far) red light reconverts P_{730} into P_{660}, which can once more be transformed into P_{730} by light (near) red irradiation, and so on.

$$\text{Phytochrome}_{660} \underset{\text{dark red (far red)}}{\overset{\text{light red (near red)}}{\rightleftharpoons}} \text{Phytochrome}_{730} \longrightarrow \begin{array}{c}\text{A}\\ \downarrow\\ \text{B}\end{array}$$

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[4] Action spectra show the relative activity of various spectral regions on the radiation-dependent physiological processes. An exact action spectrum is obtained by measuring the number of quanta of various wavelengths required to produce identical effects. The position of the action maxima provides some information on the pigments involved in absorption of the radiation, i.e., on the photoreceptors of the particular photobiological processes.

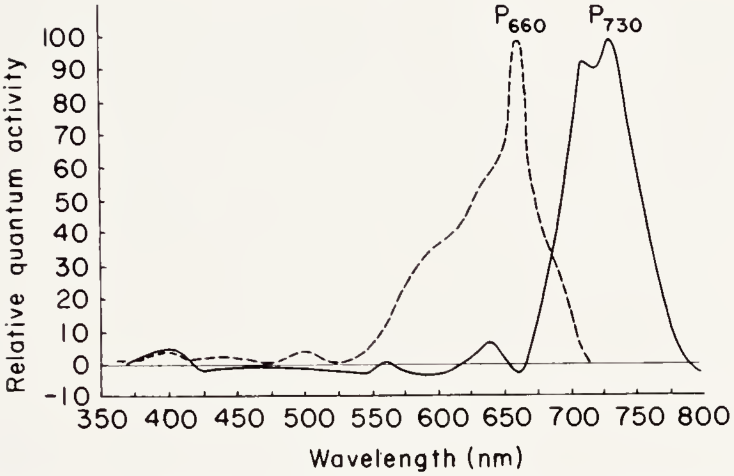

FIG. 16.14. Photomorphogenetic action spectra of phytochromes P_{660} and P_{730}. [After Withrow (1957).]

The concentration of phytochrome in plant cells and tissues is exceedingly low, but it has very recently been extracted from certain plants, e.g., maize and oat seedlings, and concentrated solutions were obtained. It has been shown in the course of this work that the reversibility is retained even *in vitro*. Irradiation of the solution with dark red light produces the blue-colored P_{660}, subsequent irradiation with light red light converts it into the greenish P_{730}. The absorption spectrum of P_{660} is very similar to that of the phycocyanins (see p. 48), especially to that of allophycocyanin. Apparently, phytochrome is a biliprotein closely related to the phycocyanins, though not identical with the latter. Isolation of phytochrome in the pure state has not so far been achieved, so that its structure remains to be elucidated.

The energy required for the activation or inactivation of the phytochrome system is small. However, the efficiency of the utilization of radiation is greater in the reaction producing P_{730} than in the reverse reaction. Thus, in ordinary sunlight, which contains about equal amounts of the light and dark red components, the active P_{730} form predominates. This apparently removes a physiological block inhibiting certain development processes opening the way for the conversion of A into B, as indicated in a general manner in the reaction scheme given above. The potential ability to carry out the reaction from A to B is, however, determined by the genetic information incorporated in the plant. In other words, it can be said that the radiation activates certain potentially active genes through the phytochrome system, in the sense that P_{730} inactivates the repressors of the respective genes (see p. 337). This example is therefore especially useful for illustrating the interaction of outer and inner factors in plant development.

Finally, it may be pointed out that many spectral regions, especially the high-energy short-wavelength regions (UV, X rays) whose mutagenic properties have already been discussed (see p. 308), can also exert a detrimental effect on plant cells. The maximum activity of the UV is often in the region of 260–270 nm, the principal absorption region of the nucleic acids, which are apparently inactivated by radiation. Other protoplast components might, however, also be involved in the absorption of radiation. At sufficiently high intensities such radiations lead to the destruction of the irradiated cells. This is utilized in the sterilization techniques in the field of bacteriology. The sunlight reaching plants contains practically no components of wavelength shorter than 300 nm.

TEMPERATURE

The development processes of plants consist of many chemical reactions, the Q_{10} values of which amount to 2 or higher (see p. 215); development can, therefore, be expected to depend on temperature. In general, it can be said that growth commences only if a certain minimal temperature is exceeded; the value of this minimum varies in individual cases. Above the minimum, the rate of growth increases with rising temperature. After the optimum is exceeded some inhibiting effects appear, which finally led to a cessation of growth. Fig. 16.15 is a typical curve exhibiting an optimum value. The temperatures corresponding to the minima, optima, and maxima, the so-called cardinal points of growth, vary for various plant species.

Temperature resistance should not be confused with the cardinal points (Fig. 16.15). While the minimum temperature for growth normally does not lie below 0°C, many plants can easily survive the effect

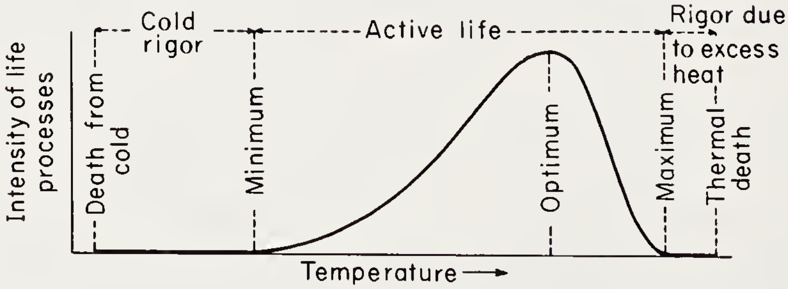

FIG. 16.15. Curve of temperature against the intensity of life processes, showing the cardinal points and points of low and high temperature death. [After Claus *et al.* (1932).]

of lower temperatures for longer periods. For example in northern latitudes many trees can survive temperatures as low as −60°C. In the dormant condition the plasma of bacteria and of spores can even survive temperatures of −273°C. A similar picture is found in the case of resistance to heat. Thus, bacterial spores are not killed by heating to 100°C, while active plasma is denatured irreversibly at only 65°C. This temperature is sufficient to kill vegetative germs (pasteurization).

Apart from these nonspecific effects, temperature can give rise to certain formative effects (thermomorphoses). For instance, low temperatures, like light, can inhibit the elongation of internodes. Potatoes do not develop tubers when the temperature is high at night. Carrots assume a conical elongated shape at lower temperatures, while at higher temperatures they become short and compact. The color pattern of many flowers can also be modified by the temperatures prevailing during a certain phase of bud development. Conditions are further complicated by the fact that the temperature requirements of one and the same organism vary in different phases of its development. Moreover, a regular night and day alternation of temperature is more favorable for many development processes than constant high temperatures. The optimum temperature at night is lower than the daytime optimum.

An important practical example of differences in the temperature dependence during various phases of development are our winter cereals. In the first phase of their development they require a low temperature. If the low temperatures are not realized (e.g., in the case of spring sowing) the cereals remain purely vegetative in their further development and do not produce flowers. Given, however, an artificial treatment at about 5°C in this stage of development, they develop normally even after spring sowing. This conversion is described as *vernalization.* Oddly enough, the low temperature treatment can in some plants be replaced by gibberellin treatment (see p. 345); the mechanism of the gibberellin action is, however, still obscure.

GRAVITY

The gravitational field is present everywhere on Earth, and its effects are therefore detectable only if the organism observed is freed from the influence of this unidirectional field. This can be achieved by letting the plant rotate around a horizontally oriented axis of a clinostat,[5] to allow the field to act on all sides symmetrically. One of the most important formative effects of gravity (geomorphoses) is the induction of dorsiventrality. It is thus possible to induce many plants, which normally develop dorsiventral flowers, to produce flowers of actinomorphic symmetry by rotation on a clinostat. The induction of polarity by the gravitational field in germinating spores has already been referred to (see p. 339). The primary effect of gravity in this case may well be an asymmetric distribution of materials inside the cell due to the gravitational field.

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[5] A clinostat is an apparatus driven by clockwork or by electricity, whose axis rotates at constant speed. The orientation of the axis with respect to the Earth's gravitational field can be varied.

CHEMICAL EFFECT

Because of their significance in plant nutrition, chemical factors (e.g., water or ions) can also give rise to formative effects (chemomorphoses). An example of this is offered by *Ranunculus aquatilis* (Fig. 7.5), whose submerged leaves are dissected while those floating on the water and in contact with the air are not (hygromorphoses). Persistent drought induces many plants to reduce the water permeability of their cortical tissues, e.g., by thickening of the cuticle, forming thorns, and increasing the development of conducting and strengthening elements.

All the examples given above support the statement made earlier (see p. 288) that the genetic information does not determine a property but only the potential for developing it; the particular characteristic then develops as a result of interaction with modifying external factors.

Rhythms of Development

During its ontogenesis the plant organism passes through a number of developmental stages which lead from the germ cell through embryonic and early stages to ripening, and finally through aging to death. This gives rise to a rhythmic alternation of developmental cycles, irrespective of whether the individual can go through the growth and reproductive phases repeatedly or only once. The cycles of development can be separated by periods of dormancy. In this case the cycle of development is coupled with a rhythmic alternation of activity, i.e., a regular alternation between active phases of life and dormant periods. Both the cycles of development and of activity are of endogenous character, but they can nevertheless be governed by external factors.

Among the best known examples of this type of behavior are the phenomena exhibiting yearly periodicity, which occur mainly in the temperate zones, e.g., the commencement of growth in spring, the autumn defoliation of many trees and bushes, and the yearly periodicity of flowering. At first sight it might appear as if this periodicity were due solely to climatic factors, i.e., exclusively external ones, but this is not the case, as shown by the example of plants which exhibit yearly climatic periodicity at our latitudes. When these plants are transferred to tropical zones, which have no pronounced periodicity of climatic conditions, they nevertheless retain their developmental and activity rhythms now no longer connected with the alternation of seasons. The length of the periods normally differs from the original 12 monthly period, which suggests that the periodic change of the phases must at least partly be due to an endogenous factor. Under the conditions of the seasonal climatic changes in the temperate regions the rhythm of the plant is governed in such a way that the phases of activity coincide with the summer and those of dormancy with winter.

This statement raises the question of how the plants recognize the various seasons. Originally it was thought that plants simply respond to the seasonal variations of certain climatic factors, such as temperature, but this only applies to some marine organisms. Only in the seas does the variation of temperature follow seasonal changes in anything like regular manner. For terrestrial plants temperature is not a reliable indication of the season, because such plants are subject to large temperature variations within days or even within hours. The only reliable indication of the season that is independent of the climatic variations is the length of the day. It has now been found that in fact many plants are able to measure the length of the day exactly, often to within minutes, and are able to regulate the course of their development by means of this "physiological clock." This phenomenon is the basis of photoperiodism.

Days of equal length occur twice a year, with the exception of the shortest and the longest day; thus, organisms must be able to distinguish periods when the day's length increases from those when it decreases, and the photoperiodic control must consequently be coupled with a second controlling mechanism. This is often provided for the plant by temperature. In many plants, such as our winter cereals, this additional blockage is removed by treatment with low temperatures of about 5°C, and the way is freed for photoperiodic control. This phenomenon has already been described by the term "vernalization" (see p. 357).

A great number of physiological processes are under photoperiodic control, such as the formation of tubers, bulbs, stolons, and frost resistance; the example chosen here for discussion is the photoperiodic control of flower development.

Taking the onset of flower formation as the criterion, i.e., the transition from the vegetative to the reproductive phase, a distinction is made between long-day plants, short-day plants, and day-neutral plants. The time of flowering of the latter is not governed photoperiodically, the long-day plants flower only when a certain minimum (critical) day length is exceeded, and the short-day plants flower only when the length of the day does not exceed a critical value. When these conditions are not satisfied, the plants remain purely vegetative. The critical day length varies for different species and is generally within the range of 10–14 hours. The short-day plants, such as rice, millet, potatoes, and some tobacco species, are natives of tropical zones and in our latitudes start their reproductive development only during the short autumn days. The long-day plants are our native cereals, lettuce, spinach, and some tobacco species.

The dependence of flower formation on the length of the day may lead to the assumption that photoperiodic control depends on the quantity of incident light and thereby possibly on the daily yield of the photosynthetic process. This, however, is not the case. The decisive factor is the duration of illumination, while the light intensity is without effect over a wide range of values as long as it exceeds a certain threshold. The threshold value is very low and amounts to only a few lux, but is significantly above the light intensity of the full moon, so that the latter cannot interfere with the measurement of the day length. The photoperiodically active radiation (see p. 361) is, as is now known, taken up by the foliage leaves; the formation of flowers, however, is not initiated by an increased rate of flow of assimilates.

On the contrary, it is assumed that a "flowering hormone" is formed under the control of the physiological clock when the day reaches the required length; this "hormone" is then transported to the growing point of the shoot and there induces the formation of flowers. This hormone does not seem to be species specific. For example *Hyoscyamus niger* (henbane), a long-day plant, begins to form flowers even under conditions of short-day illumination when a leaf of a short-day tobacco plant (a completely different plant species) is grafted on it. However, the impulse for flower formation is only transmitted when the two graft partners have grown together. It is interesting to note that several long-day plants can be brought to flowering even under short-day conditions by treatment with gibberellins. It must be pointed out in this connection that the biochemical reactions taking place during flower formation are not the same as those involved in the process of time measurement. On the contrary, the latter is a reaction system independent of flower formation and apparently of general occurrence; it acts by surmounting a physiological block when the necessary requirements are met, i.e., when the days become of the necessary length; this frees the path of the normal differentiation processes leading to flower formation.

The nature of the timing process on which photoperiodic control is based is as yet little known. A certain amount of information has been derived from experiments with interrupted illumination, as illustrated schematically in Fig. 16.16. If a short-day plant requiring a 10-hour day for flowering (Fig. 16.16A) is exposed to continuous illumination for 9 hours and to another hour's illumination during the dark period, the development of flowers is suppressed (Fig. 16.16B). On the other hand, a long-day plant which does not develop flowers on a 7-hour day (Fig. 16.16C) can be induced to bring forth flowers by illuminating it continuously for 6 hours and for an additional hour during the period of darkness (Fig. 16.16D). In these two parallel experiments, neither the amount of light supplied (which has in any case, just been shown to be irrelevant) nor the total duration of illumination differed, and yet the effects of the individual illumination regimes were entirely different. This shows that the total duration of illumination is not the decisive factor. The question is rather whether the light is available in a certain phase. The effect of the additional illumination, which need not be supplied in the middle of the dark period, is greatest if it is supplied a certain time after dark, i.e., its efficiency goes through a maximum; it can therefore be concluded that the plant measures time by means of an oscillator, which is characterized by a daily alternation of phases of varying light sensitivity. The effect of the additional light varies in magnitude depending on whether the light acts at the maximum of the

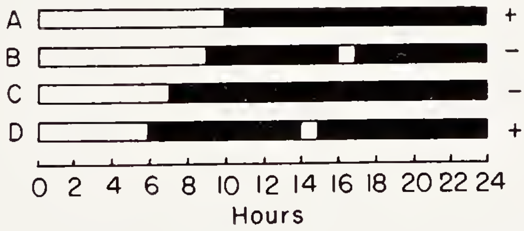

Fig. 16.16. Experiments with interrupted illumination using long- and short-day plants. Periods of illumination shown in white, periods of darkness in black. (+) Flower development proceeds; (—) flowers do not develop. (A) Short-day plant flowers in a 10-hour day; (B) flower formation is suppressed with 9 hours of continuous illumination supplemented by 1 hour of light in the middle of the dark period; (C) the long-day plant does not develop flowers in a 7-hour day; (D) the long-day plant flowers when exposed to a 6-hour day supplemented by 1 hour of light in the middle of the dark period. [After Bünning (1953, p. 454).]

sensitive phase or not. The sensitive phase always sets in after a certain period of darkness, i.e., the position of the phase depends on the alternation of light and darkness. The oscillator system is nearly independent of external factors and is therefore of endogenous character. This is also supported by the observation that the regular alternation of phases of varying sensitivity continues for a while even in continuous light or continuous darkness, though the length of the periods is somewhat modified. This can be clearly demonstrated by the daily periodic leaf movements (see p. 377), which constitute a visible manifestation of this endogenous daily rhythm.

The chemical nature of the oscillator is unfortunately at present wholly unknown. Although it is known that the radiation effective in photoperiodic control is frequently absorbed by the phytochrome system (see p. 354), this is certainly not identical with the oscillator system.

The nature of this oscillator is now the object of intensive research in the fields of medicine and plant and animal physiology because it has been shown that many physiological functions of humans and animal organisms also exhibit a daily periodicity; these, apparently, are also based on processes of time keeping. Recent studies have shown that excessively rapid and/or frequent phase displacements, caused either by regular alternation (as in shift workers) or by the necessity to adjust abruptly to different local times (which has become common in the age of jet travel), can cause certain physiological perturbations in man as well.

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Chapter 17

Movement of Plants

The widely held view according to which motion is a characteristic feature of the animals is certainly incorrect. On the contrary, plants are much more diverse than animals with respect to both the external manifestations and the mechanisms of their movement, so much so in fact that it is difficult to summarize the subject in brief. Charles Darwin wrote a very comprehensive book titled "The Power of Movement in Plants" in 1880 and his observations led to the isolation of the first growth hormones around 1910.

In plants the phenomena of motion and development cannot be distinguished as easily as in animals. Many types of plant motion are underlain by growth processes already described as integral parts of plant development, and in such cases it is difficult to decide whether an effect caused by external factors is to be regarded as a phenomenon of development, or one of motion. Quite generally, motion can be defined as a process which leads, in a relatively short time, to a visible change in the placement or position of an organ or of a whole organism.

The phenomena of motion in plants can be classified from various points of view. Induced (aitiogenic) and endogenous (autonomic or autogenic) movements can be distinguished, according to whether the movement has been caused by an external stimulus or arose spontaneously. Induced movements can be brought about by a change in the intensity of a stimulus, i.e., they can be independent of the direction from which the stimulus is acting; alternatively, the direction of the movement may be determined by the direction of the stimulus. One can accordingly distinguish between nastic movements and tropisms in localized organs, and between phobotaxis and topotaxis in the case of free locomotion. Finally, motion phenomena can also be classified according to their underlying mechanism.

Mechanisms of Motion

Motion is usually regarded as an active life process, i.e., as a manifestation of plasma activity. This view is derived from the motions of animals which are usually due to the activity of muscles or other contractile elements. This approach can also be applied to some of the movements of plants. However, a large number of other motion phenomena are known that originate from the particular structure of the plant cell walls. In such cases the motion can occur long after the death of the cell's plasma content.

MOTION DUE TO SWELLING

It has already been mentioned in the discussion of structure of the cell wall (see p. 65) that the intermicellar and interfibrillar cavities are penetrated by water molecules. In the living cell the walls are therefore in a swollen state. On death of the plasma contents they can dry out, but this process is reversible. The swelling and shrinking is always accompanied by a change in volume, the elongation and shrinkage occurring as a rule perpendicularly to the long axis of the fibrils; this necessarily results in bending and torsion effects when the axial directions of the fibrillar elements intersect in two neighboring layers. This can easily be demonstrated by appropriate models (Fig. 17.1). Such swelling mechanisms are found, for example, in the arrangements for opening of spore and seed receptacles and in the peristome of mosses (see p. 275).

Turgor motions arise due to to the variations in turgor pressure; they are therefore essentially caused by osmotic forces. As has been explained

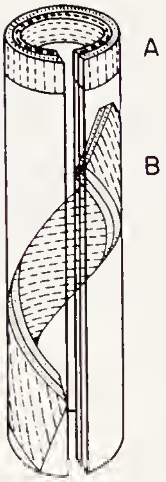


Fig. 17.1. Model illustrating the origin of hygroscopic movements: (A) bending of a two-layered band with fibrils oriented at right angles to one another; (B) bending of a two-layered band with diagonal fibrils crossing each other. (A) results in a simple bend, (B) causes a torsion effect as well. The bands of (B) can be regarded as a section of a cylinder whose fibrillar texture corresponds to the conditions prevailing in (A). [After Bünning (1953, p. 334).]

earlier (see p. 179), increased or decreased turgor can be accompanied by elongation or shortening of the cells (cf. Fig. 9.2). Consider now the case when the turgor pressure changes in the opposite sense on two opposite sides of an organ; the concomitant elongation of one side and shortening of the other may then cause bending or some other change in the position of the organ, i.e., a motion phenomenon. In principle, the turgor need only change on one side to bring about this effect.

Motion due to changes in turgor pressure is widely encountered in the plant kingdom. One example, the movements of stomata, has already been discussed (see p. 163). Due to a local thickening of the inner cell wall which holds firm, an increase in turgor leads to lateral distortion of the thin outer wall and thus an opening of the guard cell around the stoma, while a decrease in turgor results in relaxation of the outer cell wall and a closing of the stoma. A further example is that of leaf motions. These are particularly striking in *Mimosa pudica,* where they can easily be induced by mechanical effects, e.g., by a contact stimulus. As can be seen in Fig. 17.2A, the pinnae fold upward as the secondary petioles approach each other, and the primary petiole flaps downward. These motions are executed with the aid of the leaf joint (pulvinus), which consists of large, relatively thin-walled parenchyma cells and large sinuses. The vascular bundles, bordering the sinuses and usually arranged peripherally in a petiole, are here located together in a

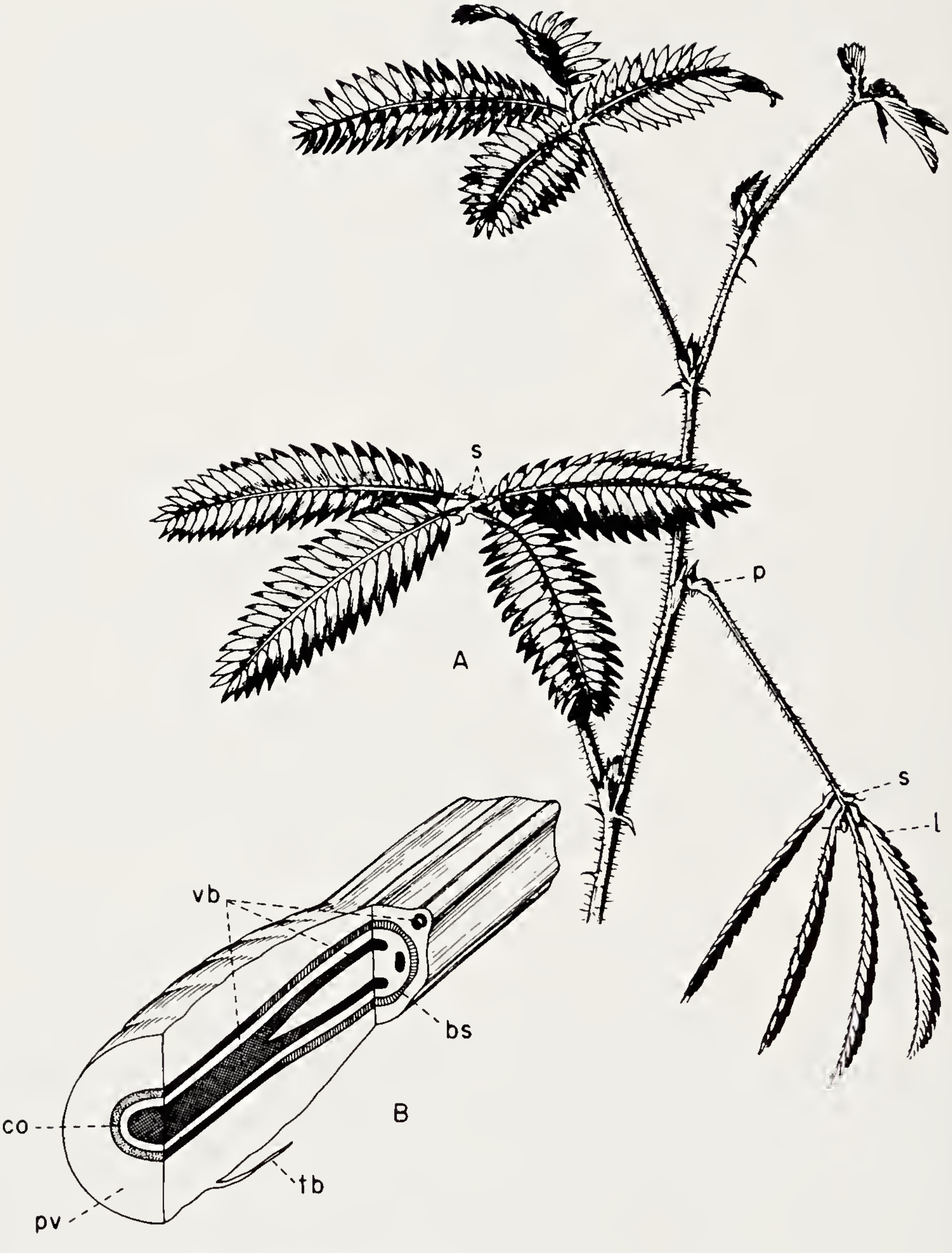


FIG. 17.2. *Mimosa pudica:* (A) shoot section with some pinnae. The leaf (1) has already reacted seismonastically (collapsed). (B) The structure of a primary leaf joint (schematic). bs, Bast sheath; tb, tactile bristle; co, collenchyma; vb, vascular bundle; p, primary joint; s, secondary joint; l, leaf; pv, pulvinus, special leaf base consisting of turgescent cells which on stimulus release water quickly into cavities or sinuses and vascular elements so leaf petiole (primary joint) and leaflets (secondary joint) collapse from lack of turgidity. [(A) after Pfeffer.]

central strand to receive the water released quickly from the pulvinus cells, resulting in the collapse of primary petiole and leaflets from lack of turgidity (Fig. 17.2B), see below.

Further movements due to turgor changes include the flapping and bending movements of the stamens (cf. Fig. 17.13) and stigma of many flowers, and the prehensile motions of the Venus flytrap (see p. 259). The latter example shows, however, that movements due to turgor may be combined with other mechanisms—growth processes in this particular instance.

Changes in turgor can arise in various ways. According to the osmotic equation of cell state (see p. 179), they may be due to changes in the osmotic pressure, which in turn can be caused by the reversible transformation of starch into sugar. Such a mechanism can, however, only account for very slow movements, such as in the opening and closing of the stomata (Fig. 17.3) exhibiting diurnal periodicity. Rapid turgor movements, such as those of *Mimosa,* occur mainly by sudden and short-lived changes in the selective permeability of the plasma boundary layers; this results in a transfer of fluid from the vacuole to the intercellular cavities and thereby in decreased turgor. The loss of fluids can be observed directly in the leaf joints of *Mimosa.* The state of hydration of the plasma (see p. 31) may also be of signficance.

The situation is very complicated when we come to consider the short-term changes in the degree of opening of the stomata; these short-term changes are not subject to daily periodicity. They are independent of the phosphorolysis of starch (see p. 226) in the guard cells, nor can they be explained by changes in permeability. Recently it has therefore been attempted to explain the origin of the changes in turgor

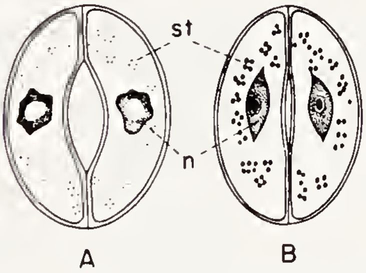


Fig. 17.3. Change in the starch content and nuclear shape in the guard cells of the stomata of *Dahlia variabilis.* (A) Stomate open. Nucleus round or irregular, with vacuole in the middle. Cell virtually free from starch. (B) Stomate closed. Nucleus spindle-shaped, with large nucleolus; numerous starch grains. n, Nucleus; st, starch. (After Weber.)

in this case by nonosmotic, i.e., endergonic, processes. Such a process might be transport of ions against concentration gradients, an active absorption of water, i.e., processes similar to those acting in the uptake and transport of nutrient salts, or CO_2 concentration. Actually the mechanism of opening of the stomata appears to be coupled with exergonic processes, both with oxidative phosphorylation and with photophosphorylation (see p. 206). Whether the state of swelling of the plasma is also involved is as yet undecided; such changes manifest themselves for instance in the alteration of the type of plasmolysis or in a change in the shape of the nucleus (Fig. 17.3).

Catapulting Movements

These movements are caused by a sudden compensation of differences in turgor pressure within individual cells or whole tissues. In *Pilobolus*, a phycomycete occurring on horse manure, a subsporangial vesicle (Fig. 17.4) develops on the sporangium holders under the sporangia containing a large number of spores; the upper part of the vesicle projects into the sporangium as a columella. In the region of the subsporangial vesicle the cell wall is extremely elastic, so that it is distended by the high internal pressure which is of the order of 5 atmospheres. Between the wall of the vesicle and the almost rigid columella there develops another elastic ring zone with a preformed tear-off point where it joins the columella. As the sporangium ripens, this ring is stretched further and further, until it is finally torn off the columella. The sudden equalization of pressure catapults the sporangium over a

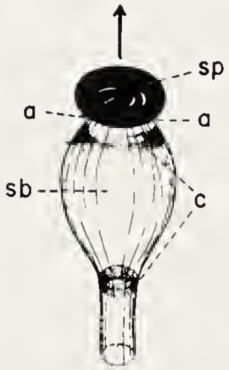


FIG. 17.4. Sporangium holders of the phycomycete *Pilobus*. The arrow shows the direction in which the sporangium is ejected after the tearing off of the subsporangial vesicle. a, Point of tear-off between the subsporangial vesicle and the columella; c, plasma zone rich in carotenoids; sb, subsporangial vesicle; and sp, sporangium.

distance of several meters. The ejection of the ascospores from the ascus is based on a similar mechanism (cf. Fig. 14.12). Finally, the tissue tensions which have already been discussed (see p. 180) can also produce such catapulting movements in the fruits of touch-me-not (*Impatiens*).

COHESION MECHANISMS

In the cases just discussed the movements were due essentially to positive wall pressure; in certain instances they can be induced by negative wall pressures as well. Such a mechanism operates in the opening of the sporangia of many ferns (cf. Fig. 14.10G,H). It has been shown that these possess a ring of cells known as the annulus, the walls of which are thickened with the exception of the external walls. After the death of their plasma contents these cells fill to capacity with water. The amount of water decreases continuously as it evaporates through the thin external walls, the external wall is pulled in as the result of the pressure deficiency due to the cohesive and adhesive forces acting between water molecules and this exerts a tangential pull on the annulus which finally allows the sporangium to be torn open at a preformed point (lip cells). The sporangium whips back forcefully and the recoil then catapults the spores for up to a meter.

MOVEMENTS OF GROWTH

As has already been mentioned, the movements of many organs may also be caused by growth processes. They arise mostly as a result of a difference in the rates of growth on opposite sides of an organ. This is shown in Fig. 17.5 on the example of a curling tendril. The acceleration of growth on the outer side of the bending organ is accompanied by a corresponding deceleration on the inner side.

Free Locomotion

Only organisms at the lower stages of organization (bacteria, algae, Myxomycetes) and certain reproductive units (zoospores, gametes) are capable of such motion in the plant kingdom. However, their mechanism is extremely varied and sometimes as yet unexplained, especially where there are no externally visible propelling organs.

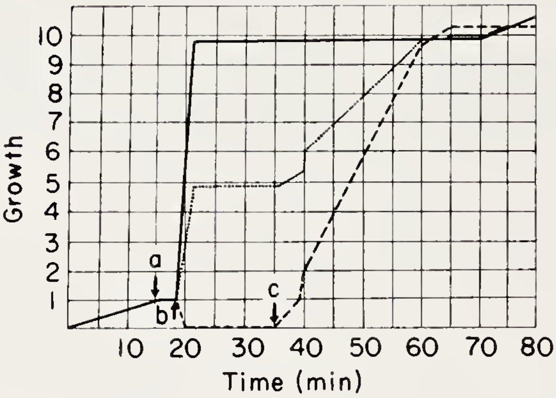


FIG. 17.5. Graphical representation of the percentage growth of the median (dotted line) and of the two opposite sides (upper side, continuous line; lower side, dashed line) of a tendril of *Sicyos angulatus*. Tendril contact with a substrate occurred after 15 min initiating the coiling process (a). (b) Start of bending as the upper side grows very rapidly while the lower (contact) side is stationary. (c) After a short pause of 15 minutes (b–c), growth of the tendril is straightening out as the lower surface now expands rapidly while the top surface is stationary.

FLAGELLAR MOVEMENTS

Flagellae are the characteristic propelling organs of the Flagellates and related organisms and of many bacteria. Many types can be distinguished with respect to the external mechanism, and certainly also with respect to the internal mechanism, of the flagellar stroke.

The situation is relatively simple in the case of the bacteria, spirillae; the bodies of these organisms are wound like corkscrews and are rather rigid. They may carry flagellae at one or at both poles, and the flagellae are not single but multiple. Rotation of these flagellae at a rate of about 40 revolutions per second causes the bodies of the organisms to rotate in the opposite direction, at about 13 revolutions per second (Fig. 17.6). Thus the organism is propelled through the water somewhat like a screw. The forward velocity can reach values of over 100 μ/sec. The volume of rotation of the flagellum then becomes bell-shaped. Reversal of the flagellar direction of rotation reverses the direction of rotation of the whole organism and so also the direction of locomotion (Fig. 17.6A–C).

In other cases, in which the body of the organism itself is not helically wound, the propeller principle is utilized. As shown by Fig. 17.7, each section of the rapidly rotating, helical flagellum develops a force, the magnitude of which depends on the gradient and which can be resolved into two components. The longitudinal component drives the body forward, while the transverse component produces rotation around the

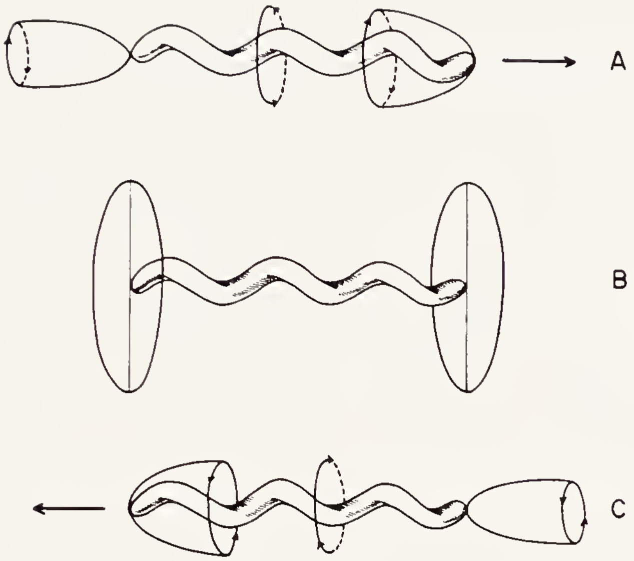


Fig. 17.6. Mechanism of motion and reversal of rotation of the flagellar tufts in bipolar spirillae. In (A) and in (C) the volume of rotation becomes bell-shaped; (B) shows the "flipping over" of the volume of rotation of the flagellae. (After Metzner, modified.)

long axis. Here too, the reversal of the direction of rotation reverses the direction of locomotion. Finally, some flagellates make use of the oar stroke principle, fully explained in Fig. 17.8. Less frequently movement is produced by wave strokes of the whiplike flagellum.

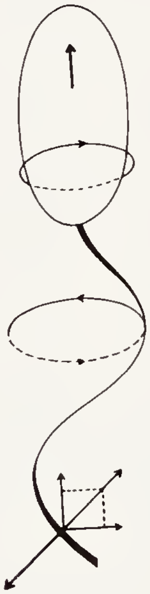


Fig. 17.7. Propulsion mechanism of the helical flagellum in *Chromatium.* (After Buder, modified.)

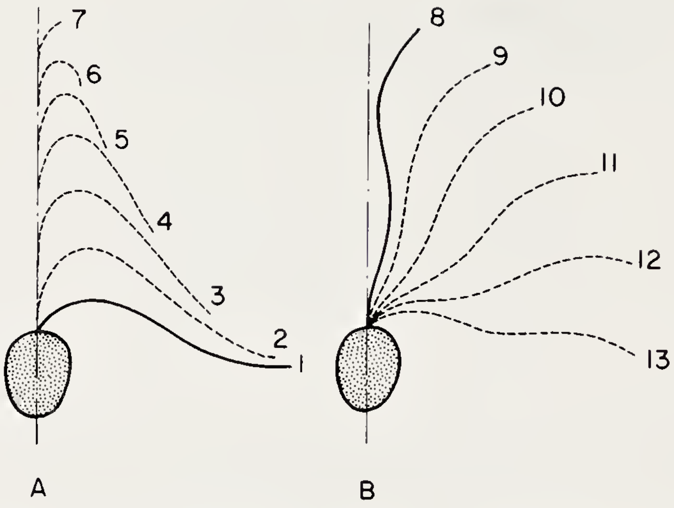


FIG. 17.8. Oar stroke of the flagellum in *Monas*. (A) Withdrawal of the flagellum to the initial position; (B) active stroke. The numbers show subsequent positions of the flagellum during a full oar stroke. (After Krijgsmann.)

Irrespective of its type, flagellar movement can only be due to rhythmic contractions of fibrillar elements which occur on either side or enclose the long axis of the flagellum. The fibrillar structure has been verified by electron microscopic studies. The flagellae of bacteria consists of only two or three fibrils, while those of the flagellates consist of eleven fibrils. As shown schematically in Fig. 17.9, two of these are arranged axially while the remaining nine are wound around them to produce a cylindrical mantle. The axial fibrils which are like elastic bars apparently serve as buttresses to the periodically contracting peripheral fibrils. The fibrils probably consist of contractile proteins which correspond to muscle actomyosin. The structural formula given below explains the way in which such a protein macromolecule may contract. Since it is possible to induce movements in isolated flagellae by ATP treatment, there is no doubt that this compound serves as an energy

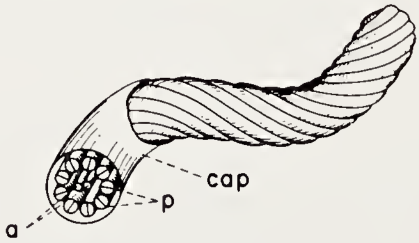
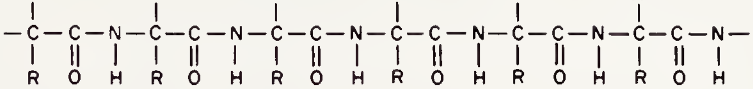
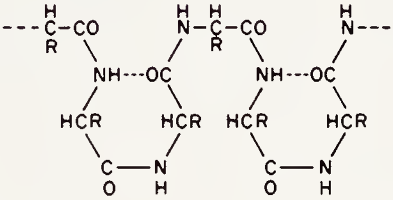


FIG. 17.9. Schematic structure of a flagellate flagellum. a, Axial fibrils; cap, capsule; p, peripheral fibrils. (After Wolken, modified.)

source during the normal movements of flagellae as well. The same should hold also for the movements of cilia.



$$-\underset{R}{\overset{H}{C}}-\underset{O}{\overset{}{\underset{\|}{C}}}-\underset{H}{N}-\underset{R}{\overset{H}{C}}-\underset{O}{\underset{\|}{C}}-\underset{H}{N}-\underset{R}{\overset{H}{C}}-\underset{O}{\underset{\|}{C}}-\underset{H}{N}-\underset{R}{\overset{H}{C}}-\underset{O}{\underset{\|}{C}}-\underset{H}{N}-\underset{R}{\overset{H}{C}}-\underset{O}{\underset{\|}{C}}-\underset{H}{N}-\underset{R}{\overset{H}{C}}-\underset{O}{\underset{\|}{C}}-\underset{H}{N}-$$



MOVEMENTS OF SPIROCHAETES

Members of the genus *Spirochaeta* possess no flagellae, and the mechanism of their motion is not yet clear for all species. They apparently make use of their body flexibility for the purpose of propulsion. The bodies of many species of these organisms are surrounded by a helically wound band of fibrils (Fig. 17.10). When this band contracts

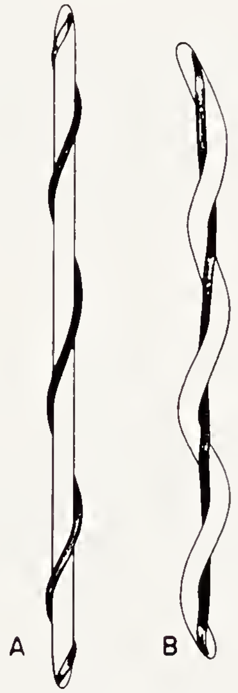


FIG. 17.10. Schematic movement of spirocaetes: (A) fibril band relaxed, body straight, elongated; (B) fibril band contracted, body deformed helically. [After Bradfield and Cater (1952), modified.]

the body suffers helical deformation, and when it relaxes the body straightens out again. Rapid rhythmic contractions enable the cell to propel itself through the surrounding medium.

AMEBOID MOVEMENTS

Ameboid movements are characteristic of the myxomycetes, but occasionally also occur elsewhere in the plant kingdom. Various types of this apparently simple propulsion mechanism can be distinguished. This type of motion is apparently largely affected by changes in the plasma viscosity due to sol–gel transformations and also by local variations in the surface tension.

SLIDING MOVEMENTS

This form of movement occurs in bacteria and also in numerous algae. Unidirectional excretion of mucous material could only be identified in certain cases; this substance swells and hence exerts a supporting effect on the cell. In the majority of cases, however, the mechanism of these movements is still obscure.

INTRACELLULAR MOVEMENTS

The changes in the position or disposition of certain cell constituents within the cell come under this heading, in particular, the migration of nuclei and plastids. In some cases they are dragged along passively by plasma currents (cf. p. 75). In other instances, such as the migration of chloroplasts caused by light (see p. 391), the plasma current explanation is not adequate.

Autonomic Movements

It has already been mentioned that many movements are autonomic, i.e., they are apparently not induced by external factors. This applies both to certain cases of free propulsion and to the movements of some localized plants. The mechanism of the movement is therefore not decisive for the autonomy of the process.

CIRCUMNUTATIONS

These are the steady circling movements of shoot apices, tendrils, and other organs. They have already been discussed (see p. 251) in connec-

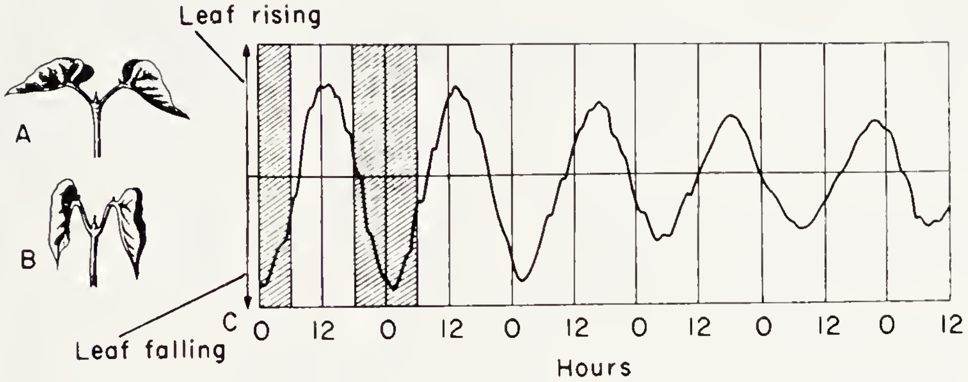


FIG. 17.11. Leaf movement of the scarlet runner bean (*Phaseolus multiflorus*): (A) position in daytime (elevated position); (B) position at night (reclining position); (C) course of the movements (schematic). The left-hand side of the curve shows normal movements of daily periodicity during the 12-hourly alternation of light and darkness (dark periods shaded). This is followed by continued movements under weak, continuous illumination; the amplitude of the periods decreases gradually and the period lengthens to about 27 hours. (After Bünning, modified.)

tion with the "searching movements" of *Cuscuta* seedlings. They are caused by a one-sided stimulation of growth along a line which encircles the axis of the organ concerned.

Movements of daily periodicity can be observed on foliage leaves and petals. These movements may be due either to growth or to changes in turgor. The latter is the case for foliage leaves which are fitted with special leaf joints (see p. 367). These are characterized by a regular alternation of a day (Fig. 17.11A) and a night (Fig. 17.11B) position, which normally follow a daily periodicity. Figure 17.11C shows this for the rise and fall of the leaves of *Phaseolus multiflorus* (scarlet runner bean). The start of the rise or fall, i.e., the phase position, is induced by the alternation of light and darkness. Nevertheless the movements are of autonomic character, i.e., they are due to rhythmic endogenous changes (see p. 362); this can be shown by keeping the plants under continuous illumination or in constant darkness after an induction period under conditions of alternate light and darkness; the movements then continue for a long time, although the length of the periods will be somewhat altered (Fig. 17.11C).

Induction of Movements by Excitation Processes

Induced movements are caused and controlled by external factors; these factors are known as stimuli irrespective of whether they are physical or chemical in nature. A stimulus consists of the delivery of a certain amount of energy, which is usually small compared with the effect it causes; it therefore acts typically as an inductor. In the so-called all-or-nothing reactions there is no relationship between the intensity of the stimulus and its result. The reaction either will take place when a certain threshold value is exceeded or nothing will happen. There are, however, certain instances in which there is a relationship between the intensity of the stimulus and the extent of the reaction; these cases will be referred to later.

In either case, however, the stimulus does not supply the energy required for the movement. It rather induces a condition of increased activity in certain plasma regions, which enables the reaction to proceed; the energy is supplied from other sources.

It may be pointed out that the induction of certain developmental phenomena by external factors is essentially a similar process. Here too the stimulus acts merely as an inductor, as has already been shown (see p. 355), while the development process itself is energetically independent of it. The effects of external factors on development and on motion phenomena are here discussed in separate chapters only for reasons of clarity.

Absorption of the stimulus and the following movement are therefore two basically distinct phenomena which need not necessarily be coupled together. The ability to react to external factors in a certain manner is one of the basic properties of the protoplasts, and it is therefore a feature of all living cells and not only of those that are capable of special reactions. In the latter the result of a stimulus is made visible by the subsequent movement, while in other cases it is not identifiable without special facilities. Such facilities include oscillographs or other sufficiently sensitive instruments by means of which the electric potentials set up at the boundary layers of cells by a stimulus can be measured.

REST POTENTIAL

As has already been mentioned (see p. 36), the plasma boundary layers of the cell and especially the plasmalemma exhibit the property of selective ion permeability. Thus, for example, the boundary layers are almost completely permeable to K^+ ions, while the permeability to Ca^{2+} and Na^+ is restricted. With the aid of active, i.e., endergonic, processes, negative chloride ions are continuously transferred from the outer medium into the cell, and cations are transferred in the opposite direction.

The mechanism of these so-called ion pumps is as yet unknown. The extent of the participation of mass flow and active transport processes and of concentration and potential differences in the migration of the various ionic species across the membranes is also uncertain at the present time.

The active transport, on the one hand, and the differences in the mobilities of the various ions, on the other, result in the development of a potential difference between the positively charged exterior of the cell and the negatively charged interior: This is known as the rest potential (Fig. 17.12A). The membrane is therefore polarized. The magnitude of the rest potential depends on the experimental object, on

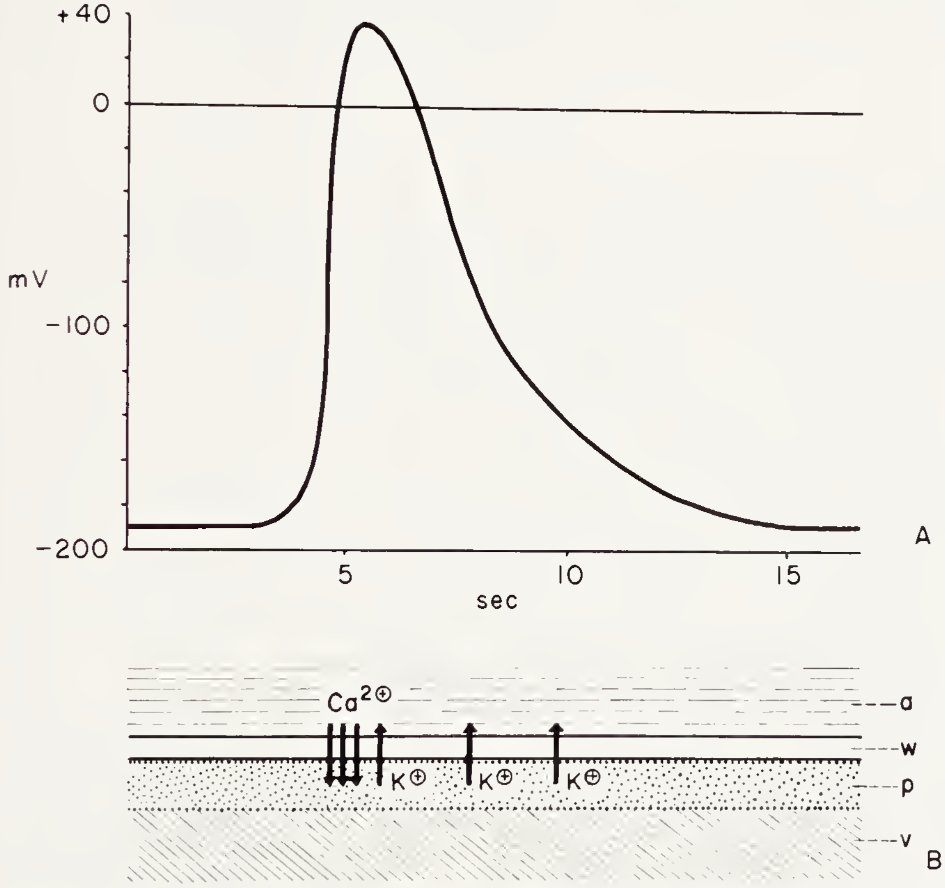


Fig. 17.12. (A) Action potential of a plant cell (*Chara*). Rest potential —190 mV, action potential 228 mV. After crossing the zero line, the inner side of the plasma boundary layer assumes a transient positive potential. (B) During the rising branch of the action potential Ca^{2+} ions enter the cell. The subsequent exit of K^+ ions reestablishes the rest potential. Finally, ion pumps remove Ca^{2+} ions and bring in K^+ ions until the original position is reestablished. a, External medium; p, plasma; v, vacuole; w, cell wall.

its physiological condition, and on the experimental conditions. Its values are of the order of 50–200 mV, i.e., the cell interior is at a potential of −50 to −200 mV with respect to the exterior.

EXCITATION PROCESS

Local stimulation of a cell whose boundary exhibits a rest potential by electrical, mechanical, or chemical effects induces an excitation process provided that the stimulus is sufficiently strong. After a short period of latency, which is of the order of 0.1 sec, there follows a temporary alteration of the membrane permeability, resulting in a sudden influx of Ca ions into the cell (Fig. 17.12B). This makes the inside of the membrane less negative, or even positive, with respect to the outside, i.e., the potential difference is dissipated and the charge on the membrane changes sign for a short while (Fig. 17.12A). This is known as the action potential. The magnitude of the action potential is independent of the strength of the stimulus, but in order to induce an action potential at all the stimulus must exceed a certain threshold value. The excitation process therefore follows the all-or-nothing rule. The influx of Ca ions is followed by exit of potassium ions (Fig. 17.12B), which continues until the rest potential is reestablished (Fig. 17.12A). Finally, the action of the ion pumps reestablishes the original situation.

A second stimulus immediately following the first one induces no reaction as the membrane is not yet polarized. The cell shows refractory behavior. This so-called absolute refractory phase is followed by a phase of reduced sensitivity, the relative refractory phase. The latter is characterized by an increased threshold value, i.e., the intensity of the stimulus must be higher than it was the first time in order to induce the reaction. The cell is fully excitable only after the lapse of the relative refractory phase.

The excitation process of plant cells is therefore basically similar to nerve stimulation in animals. One substantial difference between them is that in nerves, the role of Ca ions is taken over by Na ions. Also, the changes of potential may last as long as 20 sec in plants, while in animals they last for only fractions of a second; the refractory stages are correspondingly shorter too. The action potentials in plants are generally higher than in animals.

CONDUCTION OF THE EXCITATION

The excitation process does not remain restricted to the stimulated site but spreads in wavelike fashion over the whole cell. It can affect neighboring cells and propagate over a certain distance. This process is known as conduction of the excitation. The formation of special substances of excitation has also been confirmed; these not only distribute themselves at the plasma boundary layers but are also transported along certain conduction paths and thus transmit the excitation over longer distances. Their chemical nature is still obscure.

The conduction of excitation over longer distances can be followed especially well on objects in which the excitation is accompanied by a motile reaction. One example is *Mimosa,* in which the pinnae close one after the other at a rate depending on the speed of conduction of the excitation (Fig. 17.2A). In *Mimosa* this speed is about 2.5 cm/sec; in other plants, however, such as the quick-reacting Venus fly-trap (see p. 259) it can reach 20 cm/sec. These values border on the lower conduction velocities in many animal tissues.

MOTILE REACTIONS

As has already been mentioned, the excitation processes just described are not directly connected with motile reactions. Such reactions can only occur when the excitation process affects cells that are capable of motion because of their special anatomical features. Several such cells are often joined into a motor system, as in the leaf joints (Fig. 17.2B).

A relationship between excitation processes and motile reactions has been confirmed in a number of motion phenomena in plants, e.g., in some rapid turgor movements such as the leaf motions of *Mimosa* (see p. 367), the hinge-trap mechanism of the Venus fly-trap (see p. 259), or the nastic reactions of many stamens (see below). In these cases there is a far-reaching correspondence between the course of the induction processes and the terminology, on the one hand, and the excitation process, on the other. Between the stimulus and the motile reaction there is a time interval (lasting 0.1–1 sec) in which nothing visible happens and which is the period of latency. This is followed by the motion itself, which usually reaches a maximum in a very short time (Fig. 17.13), and by the regenerative process which gradually reestablishes the original conditions. The regenerative process takes a longer time, varying from case to case. A fresh stimulus received during this period either produces a weaker reaction or no reaction at all (Fig. 17.13). A relative and an absolute refractory phase can therefore be distinguished in this case as well.

In order to avoid confusion it must be pointed out again that there are many plant movements which are apparently not induced by any

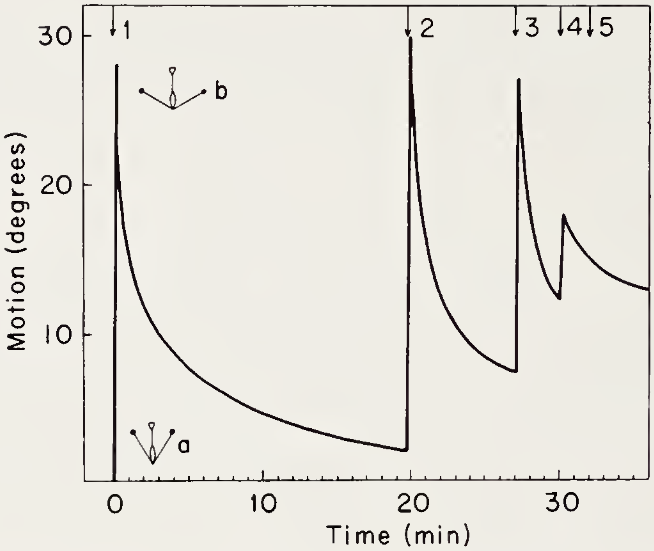


FIG. 17.13. Motile reactions of the stamens of *Helianthemum* following multiple mechanical stimulation. For the first reaction the original (a) and the final (b) positions of the anther filaments are shown. The latency period is here so short (about 1 sec) that it could not be shown in the diagram. The second stimulus occurred outside, and the third and fourth stimuli during the relative refractory period. The fifth stimulus, which fell in the absolute refractory period, did not produce a response at all.

excitation processes. The primary phenomena inducing motions in plants are still in any case rather obscure, and no general statements can be made on the subject. There is much scope here for future research.

Radiation Effects

Many induced movements, like formative effects, may be influenced in various and lasting ways by radiation. The active region of the spectrum again includes, apart from the visible range, the neighboring regions of lower or higher wavelengths, i.e., the ultraviolet and infrared regions.

PRIMARY PROCESSES

As has repeatedly been emphasized, radiation can only be effective if it is absorbed. However, not all radiation regions are equally effective, regions of stronger and weaker activity being distinguishable in the action spectra (see p. 354) of the respective motor reactions. This indicates that here, too, the radiation is absorbed by specific pigments, known generally as photoreceptors.

The absorbed radiation can become active in various ways. If the photoreceptor molecule is also an enzyme, it may be activated by the radiant energy and catalyse a reaction leading finally to a certain motion process. This mechanism, which would be similar to the action of the phytochrome system (see p. 354), could for instance apply to the flavine enzymes which are yellow and absorb radiation selectively even within the visible region. Another possibility would be for the photoreceptor molecule to act as a sensitizer; it would then transfer the absorbed energy to another system, like certain accessory pigments in photosynthesis, and thereby initiate a reaction chain. Finally, the absorption of radiation could occur via a photochemical reaction system not directly connected with the respective motor reaction, i.e., the movement could be coupled to another reaction system such as photosynthesis.

Corresponding to the different action mechanisms of the photoreceptors, the energy requirements of the individual motor reactions can be quite variable. When the absorption of radiation acts merely as an inductor for the motor reaction, the required quantity of energy is relatively small. If, on the other hand, the absorbed energy actually supplies the motor reaction, which may be the case for some reactions coupled with photosynthesis, the energy requirement is obviously much higher.

There are many ways in which radiation can be absorbed and become effective; it is therefore possible to analyse each individual case exactly, but not to treat radiation in any general way. Moreover, since the movement mechanisms may be quite different, regardless of the external similarity or identity of the individual reactions, the usual classification of movements according to the external appearance of the reaction must necessarily be incomplete. Its value today is only that of a didactic auxiliary device.

Orientation Movements

Orientation movements are among the most striking phenomena in plants caused by light: The organisms orient themselves according to the direction of the incident radiation. The condition for the perception of the direction of illumination is a fall of the intensity of light in the cell or organ concerned. The colorless cytoplasm hardly absorbs visible light and cannot, therefore, produce a sufficiently high intensity gradient; for this reason many organisms make use of screening substances. These exhibit approximately the same spectral absorption as the photoreceptor and produce an intensity gradient across an organ or an organism by partial absorption of the effective radiation.

It is usual to describe the radiation-induced orientation movements of stationary plants and their organs as phototropism, to distinguish it from the movement of motile organisms which are known as phototopotaxis.

Phototropism

Phototropism is a bending or other alteration in the position of an organ of a stationary plant regulated by the direction of the incident radiation. Normally the stem axis "turns" toward the source of light, i.e., reacts positively. The roots either behave neutrally or react in a nega-

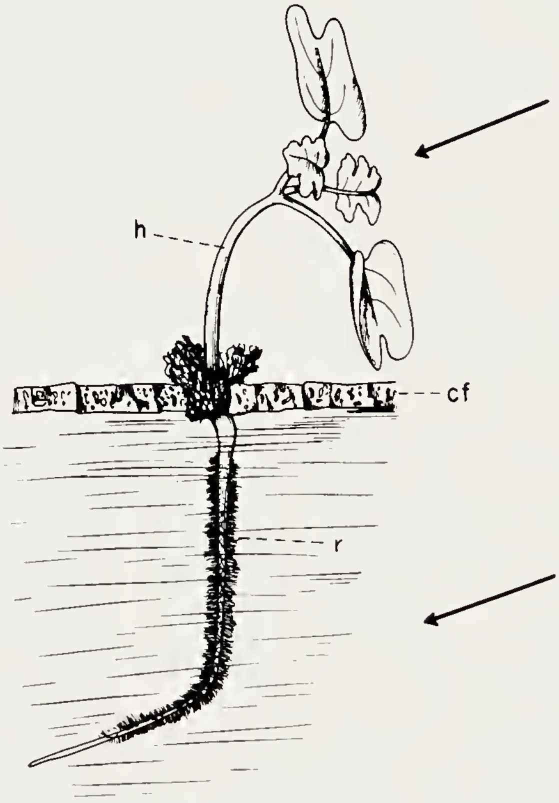


FIG. 17.14. Phototropic reaction of a mustard seedling (*Sinapis alba*) floating in a nutrient solution, fixed to a piece of cork. The hypocotyl has reacted positively and the root negatively. The leaves exhibit transversal phototropism. Arrows show the direction of the incident light. h, Hypocotyl; cf, cork float; r, root. (After Noll.)

tive manner (Fig. 17.14). Leaves arrange themselves mostly at right angles to the direction of the incident radiation; this is known as diaphototropism or transversal phototropism.

In no case has the causal analysis of a phototropic reaction so far been completely successful. Not even the mechanism of motion has been fully clarified. There is no doubt that the phototropic bending is also due to unequal growth on opposite sides, but turgor reactions may also be involved, at least in some cases. The two mechanisms may overlap, making the character of phototropic reactions very complicated indeed. Such is the case, e.g., with the coleoptile of *Avena* (oats) which surrounds completely the primary leaf of the germinating plant in its first phase of development. According to the quantity of energy received on irradiation, this sheath bends phototropically, either positively or negatively. In the low-energy region, the light sensitivity is essentially restricted to the outer tip of the organ, while the perception of higher radiant energies, leading to a reaction, occurs throughout the organ.

These two modes are usually described as apical and basal reactions, although such a division does not really reflect the true state of affairs.

Although it has been known for a long time that phototropic bending is induced only by radiation of short wavelengths, i.e., blue, violet, and ultraviolet, the mechanism of the absorption of this radiation is still unclear. Originally it was assumed that certain carotenoids act as photoreceptors, since the absorption spectra of such compounds, especially that of β-carotene, agree rather well with the phototropic action spectra (Fig. 17.15). However, the known carotenoids do not absorb significantly in the UV region of about 370 nm, which is phototropically very active. The action of other photoreceptors has therefore also been considered, such as riboflavine which exhibits an absorption maximum in this spectral region (Fig. 17.15). It has, however, only one absorption maximum in the blue region, and is therefore hardly sufficient to explain the action spectrum which has three maxima in this region. A third hypothesis attempts to overcome these difficulties by assuming the existence of a two-pigment system in which one substance (riboflavine) acts as a photoreceptor while the other (carotene) acts as a screening pigment to produce the required loss in intensity between the two sides of the irradiated organ. It is however, doubtful whether a compound acting merely as a screening substance would be able to transform the absorption spectrum of the photoreceptor exhibiting one maximum into a spectrum showing three maxima.

The problem of the way in which the absorbed radiation becomes active has also remained open. It has been assumed for a long time

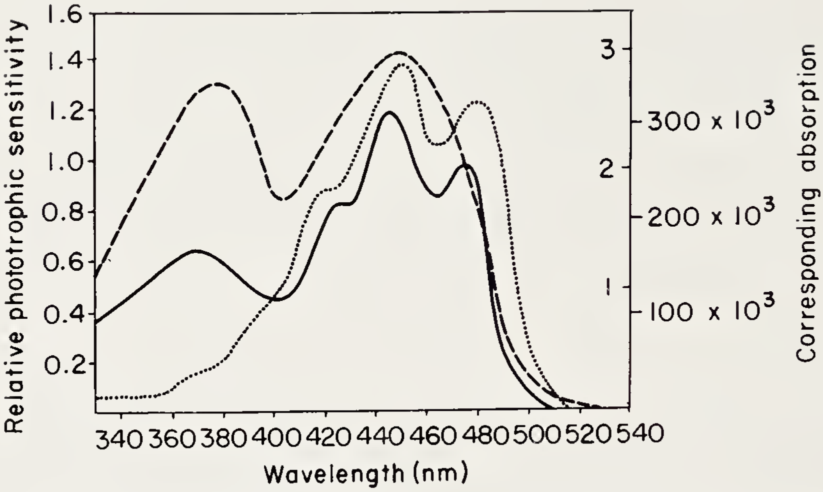


FIG. 17.15. Action spectrum of the phototropic sensitivity of the coleoptile of *Avena* (continuous line). The absorption spectra of β-carotene in hexane (dotted line) and of riboflavine (dashed line) are given for comparison. (After Curry and Thimann; Karrer and Jucker; Bellin and Holmström.)

that phototropic bending is caused by a difference in light-induced growth between the illuminated and the dark sides of the organ.

The term light-induced growth reaction (LGR) describes the change in the rate of growth caused by a change in the intensity of incident, nonoriented radiation. The increase in intensity may cause an increase in the rate of growth, as in the sporangium holders of phycomycetes; this is known as positive LGR. The organs may, however, reduce their rate of growth when the light intensity increases, as is the case for the coleoptile of *Avena*, and the LGR is then said to be negative. The LGR is due mainly to a change in the plasticity of the cell wall caused by the radiation. Details of this phenomenon are still unknown.

Attempts have been made to explain the positive phototropic bending of the sporangium holders of the phycomycetes as follows, on the basis of a positive LGR: The colorless, cylindrical sporangium holders, which act like a convex lens, collect the radiation coming from the sides onto the dark side into a focal line which is thus illuminated more brightly than a corresponding area at the front. The stronger LGR of the reverse side caused by this effect would accelerate the growth of that side and would cause the organ to bend toward the light. The connection between LGR and phototropic bending is also supported by the observation that both reactions have the same absorption spectrum, i.e., they proceed through the same photoreceptor system. Recent investigations have shown, however, that LGR is neither a necessary nor a sufficient condition for the induction of phototropic reactions.

The only consequence of one-sided irradiation of the organs of higher plants that has so far been established beyond doubt is the alteration of auxin content of the illuminated and dark sides. This can be demonstrated as follows on *Avena* coleoptiles (Fig. 17.16): An *Avena* coleoptile is illuminated from one side, the outer tip is cut off, and is transferred onto an agar cube cut in half; the auxins flowing downward from the tip diffuse into the agar, and the auxins from the light and dark sides of the tip are thus separated. The two agar cubes are now placed on top of one side of decapitated coleoptiles (Fig. 17.16); under these conditions, only one side of the coleoptiles receives growth substances (which are basipetally polar) from the agar blocks which leads to a bending of the coleoptiles. The bending caused by the block having received auxins from the dark side is larger (Fig. 17.16), and this block must therefore have a higher auxin content (i.e., more auxin must have flowed down the dark side of the coleoptile than the illuminated side). The auxin asymmetry in the organs illuminated from one side is probably produced by diversion of the auxin flux from the light to the dark side, but the possibilities of auxin inactivation on the illuminated side and auxin activation or increased auxin production on the dark side have also been considered. Since the sporangium-holders of the phycomycetes do not react to a one-sided application of auxin, the auxin-

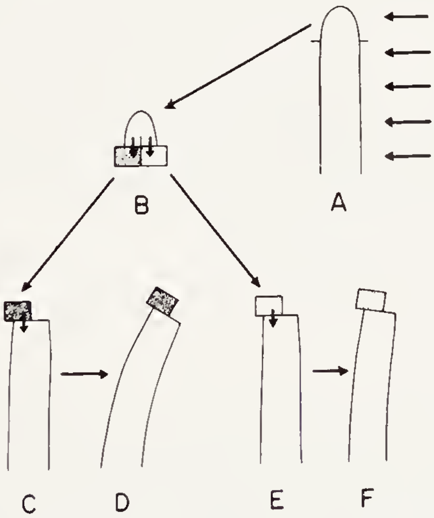


Fig. 17.16. Effect of one-sided irradiation on the distribution of auxin in an *Avena* coleoptile. The coleoptile is irradiated (A) and then decapitated; the tip is placed on a cube of agar (B). More auxin diffuses down into the agar on the dark side than on the illuminated side. The two halves of the agar cube are then placed on one side of decapitated coleoptiles; this results in bending of the coleoptiles to various extents, depending on the auxin contents of the agar cubes (C—F).

transfer theory is not sufficient to explain their phototropic reactions. Phototropism therefore still involves many unsolved problems.

Phototopotaxis

Corresponding to phototropic bending, the orientation movements of freely mobile organisms lead to an approach or escape from the source of light, depending on whether their reactions are positive or negative. In these reactions, too, short-wavelength radiation is usually (though not always) most effective. The parallelism with phototropism is obvious. The way in which the light controls the movements has only been clarified to some extent for the green flagellates and zoospores. These possess next to the point of attachment of their flagellum a stigma (Fig. 5.5), which is red due to the presence of carotenoids. When radiation impinges from the side on such an organism in motion, the stigma is interposed between the light source and the base of the flagellum (which can be regarded as the seat of the photoreceptor) at regular intervals owing to the regular rotation of the body around its long axis. The resulting periodic shadings cause the stroke of the flagellum to vary, and the long axis of the body is turned increasingly toward the light source. Repetition of this process finally orients the organisms so that the light rays strike them from the front, when the stigma no longer shadows the base of the flagellum. The flagellate therefore swims on in a straight line toward the source of light.

The negative reaction is often observed in the same organisms at high light intensities. The mechanism described above would apply to this case, too, but the flagellar stroke would now be altered so as to turn the organism in the opposite direction; it would then eventually swim away from the source of light.

REACTIONS DUE TO VARIATIONS IN THE LIGHT INTENSITY WITH TIME

Orientation movements apart, there is a whole group of motor reactions caused by changes in the radiation intensity with time, and which are unaffected by the direction of incidence of the radiation. They also occur when the incident light is diffuse. In some cases it is also relevant, whether the change in the light intensity occurs suddenly or gradually.

Photonasty

Photonasty is the motion of a stationary organ caused by changes in light intensity but independent of the angle of light incidence. The independence of the direction of incidence is mainly due to the anatomy of these organs, which determines unambiguously the direction of motion (hinged movements). Here, too, the motion can be due either to growth or to turgor effects.

The movements of the stomata can be regarded as photonastic. The conditions in this case are rather complicated, in that the opening and closing process is governed not only by light but also by temperature (thermonasty), atmospheric humidity (hygronasty), and also by chemical factors (chemonasty) such as the CO_2 concentration. The mode of action of all these factors is as yet wholly unclear.

In many cases the effect of the radiation is proportional to its absorption by chlorophyll; it has therefore been previously assumed that the osmotic value of the cell sap increases due to the production of sugars by photosynthesis, and that the bending of the guard cells and opening of the stomata is caused by the consequent increase in turgor. However, the situation cannot be as simple as that, because the daily photosynthetic yield of a guard cell is insufficient to produce the required increase in the osmotic value. According to another view, the pH increases owing to photosynthetic utilization of CO_2 and simultaneous loss of CO_2 from the plasma; this would activate the phosphorylases, which maintain the equilibrium between starch and sugar, and would cause some starch to be converted into sugar. According to what has been said about the opening mechanism of the stomata (see p. 369), the starch–sugar conversion mechanism could only account for the slow diurnal changes in the gap width of the stomata. Radiation could intervene in the fast changes in the gap width, which are induced by variations in the external factors, through the process of photophosphorylation. Since the latter is influenced by temperature and by the CO_2 concentration, this could explain both the temperature and the CO_2-concentration dependence of the degree of opening of the stomata. The availability of water, on the other hand, would directly affect the turgor pressure.

Photophobotaxis

In many motile organisms sudden changes in radiation intensity may cause an alteration or reversal of the direction of motion. This effect is independent of the direction of incidence. The change in the direction of movement is often preceded in organisms provided with flagellae by a sudden circulating movement that has been described as a phobic reaction (hence "phobo" taxis). A phobic reaction following a decrease in intensity is said to be positive, and one following an increase in intensity negative.

Under conditions of nonhomogeneous illumination, which can be arranged by projecting a light beam into a dark chamber, the behavior described above leads to an accumulation of organisms in the light beam if the reaction is positive (light trap) or to a depopulation if the reaction is negative (Fig. 17.17), according to whether the organisms reverse the direction of their movements when entering the dark or when entering the light region. The mechanism of the reversal of the direction of movement has already been discussed (see p. 373 and Fig. 17.6).

In the purple bacteria and the Cyanophyceae the spectral regions absorbed by the pigments of the photosynthetic apparatus are also active phobotactically. In these organisms, the processes of photosynthesis and of photophobotaxis are coupled. The relationship between these processes could be explained as follows: A sudden drop in radiation intensity would cause an abrupt decrease in the electron flux in the photosynthetic electron transport chain (see p. 208). When the difference was large enough, it would induce a switching process, similar to a relay, which would operate the momentary switching over of the motor apparatus. Negative reactions, which occur most frequently at light intensities exceeding the saturation value of photosynthesis, could be produced by a sudden increase in the electron flux.

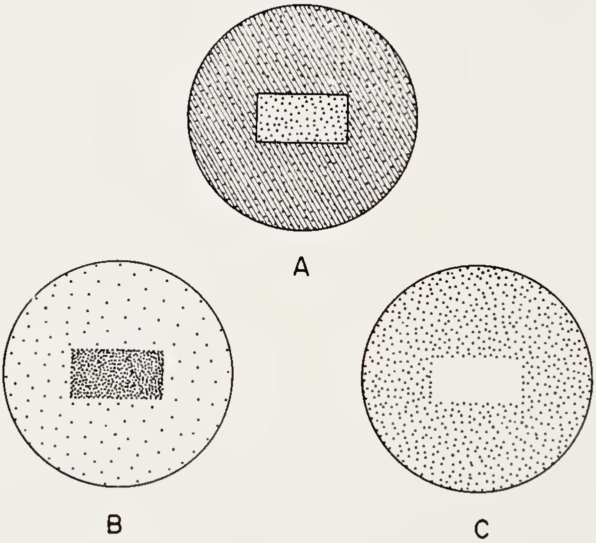


FIG. 17.17. Demonstration of photophobotaxis by means of a light trap. (A) A beam of light is projected onto a preparation in which the organisms are distributed evenly (the dark background is shaded). (B) Positive reaction: The organisms gather in the light beam. (C) Negative reaction: The organisms leave the illuminated region.

For other organisms, such as the flagellates and green zoospores, in which the spectral regions of photophobotactic sensitivity and photosynthetic activity do not overlap, another operating mechanism must be assumed. The phobic reaction could here be due to reduced illumination or shading of the bases of the flagellae.

Photokinesis

In many motile organisms the light affects the speed of the motion or even initiates it in the first place. This is known as photokinesis. Most frequently the phenomenon observed is positive photokinesis, i.e., the light speeds up or induces the movement. Cases of negative photokinesis are, however, also known; for example, rigor due to excessive light intensities. Recent studies have shown that the radiation acts through photophosphorylation, i.e., positive photokinesis is a result of increased production of ATP. In this case the radiation in addition to inducing the motion supplies the energy required for its execution.

EFFECTS OF RADIATION ON INTRACELLULAR MOTIONS

The movements of the plasma and of many cell constituents, known as intracellular movements or protoplasmic streaming, can also be affected by light. Thus, it is known that in the cells of many plants toward a strong incident light (cf. Fig. 3.7A). The mechanism of these movements depend to some extent on the intensity and duration of the illumination. Such effects of light are known as photodineses.

Movements of Chloroplasts

In the cells of many plants irradiation induces movements of chloroplasts which result in the development of characteristic arrangements of these organelles in the cell. In the typical case two positions can be distinguished: a weak and a strong illumination position. In the former the chloroplasts arrange themselves in a plane approximately perpendicular to that of the incident light (Fig. 17.18B) for best light utilization; in the latter, the chloroplasts are arranged along the cell walls which are parallel to the direction of the incident light (Fig. 17.18A). In the alga *Mougeotia*, the plate-shaped chloroplasts turn their faces toward the incident radiation if this is weak while the edge is turned toward a strong incident light (cf. Fig. 3.7A). The mechanism of these motions is almost completely unknown (see p. 376). In *Mougeotia* the radiation acts via the phytochrome system (cf. p. 354).

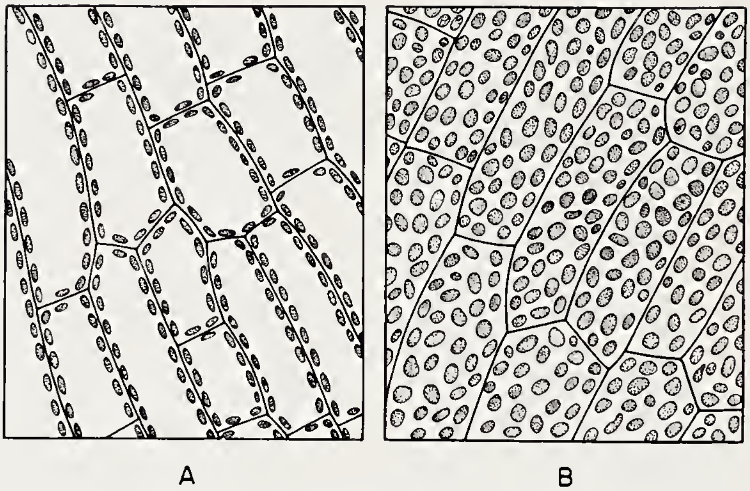


Fig. 17.18. Chloroplast movements induced by light in *Funaria hygrometrica.* Cells from the leaf, viewed from above. (A) Leaf after 24 hours in the dark; the chloroplasts are all along the side walls. This is also the strong illumination position. (B) Weak illumination position, in diffuse daylight. The chloroplasts are all at the outer walls. (After a photomicrograph by Bünning.)

Gravitational Effects

Apart from light, the gravitational field is the other important factor that can influence many plant motions. Motor reactions of stationary organs in response to gravitational stimuli are known as geotropism, and the corresponding reactions of motile organisms are known as geotaxis. Geotaxis is much rarer and is of much less importance so that only the geotropic phenomena will be discussed here.

GEOTROPISM

The orientation of organs parallel to an axis through the center of the Earth, such as is normally found in the shoot axes and main roots, is known as orthogeotropism. The reaction of the roots is positive, i.e., they grow toward the center of the Earth, while the shoots react negatively, i.e., they grow away from the center. Some organs orient in a plane inclined at an angle to the perpendicular, e.g., the side roots of first order, many rhizomes, and side shoots. This is known as plagiogeotropism. A special case of this behavior is diageotropism, in which the angle is 90°; the long axis of the organ is then at right angles to the perpendicular.

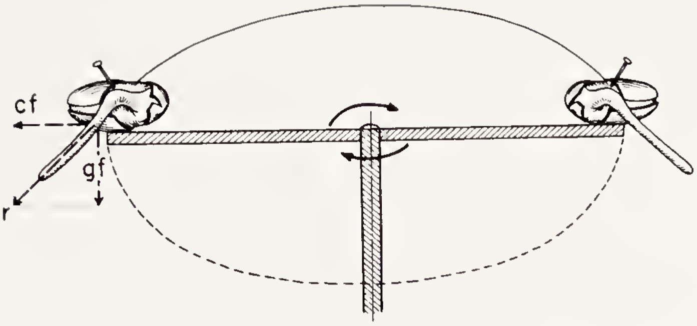


FIG. 17.19. Growth of the roots of *Vicia faba* on a centrifugal apparatus (after Knight). In this case the centrifugal force (cf) was equal to the gravitational force (gf) so that the roots (r) have oriented themselves at an angle of 45° to the perpendicular.

The possibility of replacing gravity with centrifugal force indicates that geotropism is caused by the sensitivity of the organ concerned to an accelerating force. Seedlings may, for instance, be fixed to a disk rotating on a horizontal axis; the roots then grow outward, corresponding to the centrifugal force, while the shoots grow toward the disk's axis. The axis of the apparatus may, however, be oriented vertically, so that the plants on the disk rotate in a horizontal plane; the long axes of the shoot and the root then orient themselves at a certain angle to the perpendicular. The magnitude of this angle depends on the magnitude of the acting centrifugal force relative to the force of gravity. According to the size of these two vectors the organs orient themselves along the direction of the resultant force, which follows from vector addition of the acting forces (resultant rule).[1] If the centrifugal and gravitational forces are equal, the angle is 45° (Fig. 17.19).

According to the sine rule g sin α (Fig. 17.20), the influence of the force of gravity on an organ growing orthogeotropically increases with its displacement from the normal position, i.e., with increasing angle α between the long axis of the organ and the perpendicular. It is thus strongest when $\alpha = 90°$. This relationship holds, however, only in the neighborhood of the threshold value of the stimulus. With increased time of action of the gravitational forces, the action of other forces,

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[1] The resultant rule also applies within limits to the responses to other stimuli. Thus, if an organ is irradiated by two light sources simultaneously, so that the two beams reaching the organ are at an acute angle, the plant will react phototropically by bending in the direction of the resultant which can be worked out from the directions and intensities of the two beams by vector addition. There are, however, certain organs which react phototropically but do not follow the resultant rule, e.g., the sporangium holders of the phycomycete *Pilobus*.

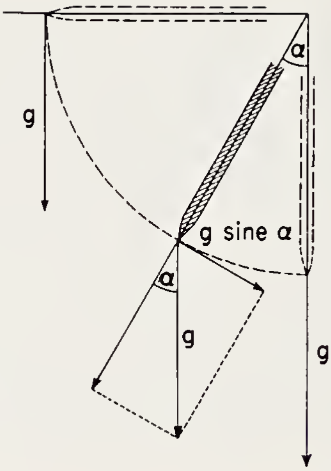

FIG. 17.20. Action of gravity on a root which deviates from the direction of the gravitational force (g) by an angle (α). The geotropically active component is g sine α (sine rule). (After Sierp.)

acting along the long axis of the organ, becomes appreciable. The forces inhibit the geotropic reaction when the deviation in the orientation of the organ from the normal position is less than 90°, but enhance the reaction when the organ approaches the inverse position of 180° displacement, i.e., at displacements exceeding 90°. Thus the geotropic induction is most intense when the position of the organ is in the range of 125°–135°.

Present-day views of the processes operating in geotropic induction are still largely hypothetical. It is certain that an asymmetric distribution of growth substances occurs in a geotropically active position; the concentration of such substances being smaller in the upper side of the organ and greater in the lower side. The total concentration of growth substances is normally suboptimal in shoots and just above the optimal in roots. Thus, an increased concentration on the underside of the organ leads in the case of the stem to an approach to the optimum, stimulation of growth of the lower side, and thus to an upward bending of the organ. In the case of roots, on the other hand, it means a departure from the optimum, i.e., inhibition of growth of the lower side and thus a downward curvature of the organ. It is not yet certain whether this is due to a transfer of the growth substances at an oblique angle to the long axis of the organ, to one-sided activation of the growth substances, or to renewed formation of such substances. It is also doubtful whether the asymmetric distribution of growth substances which can only be observed after long periods is itself the primary process, since geotropic bending can be induced by short-lived effects of gravitational forces, lasting only a few minutes.

The question of how the geotropic stimulus is perceived in the first place has been answered in various ways. According to the statolith theory, the primary effect consists in a displacement of small cell inclusions, which resemble the statoliths found in animals. Starch grains, common in geotropically reacting organs (root caps, endodermis of shoot axes), are often suspected of being involved; these undergo changes of position corresponding to the action of gravitational forces under geotropic stimulus. The starch grains are supposed to exert a mechanical stimulus on the corresponding parts of the protoplasts, which induce all the reactions that follow. However, since some organs not containing starch also exhibit geotropic reactions, statolithic function has also been ascribed to other cell organelles, such as the mitochondria.

According to another hypothesis, the primary effect of the gravitational force consists in inducing a potential difference between the upper and lower sides of the organ being stimulated; this effect would be caused by the difference in the action of the gravitational force on the mobility of cations and anions (geoelectric effect). The potential difference would then induce, among others, a quasi-electrophoretic migration of the plant hormone molecules.

Finally, differences in suction force between the upper and lower sides of organs in a gravitational field have also been observed (geosuction reaction), which could be identified after only a few minutes of stimulation.

Plagio- (at an angle to perpendicular) and diageotropism (90° to perpendicular) can only be explained as the result of two counteracting components. These could both be of the geotropic kind, i.e., positive and negative geotropism, or, alternatively, the negative geotropism can be counteracted by an always present tendency of the upper sides of organs for excess growth, known as epinasty; this is the case in many leaves. Epinasty is independent of geotropism and, therefore, does not lose its activity when the one-sided stimulus is removed by rotation of the plant on a clinostat. That is why leaves bend upward with respect to the long axis of the shoot in the absence of a counteracting negative geotropic component.

Chemical Effects

Chemical stimuli can induce both oriented movements (chemotropism, chemotopotaxis) and movements whose direction is independent of the stimulus gradient (chemonasty, chemophobotaxis). The first type is an active reorientation corresponding to an existing concentration gradient; the second is a reaction in response to concentration differences. However, the two cases cannot always be clearly distinguished, at least in the case of chemotaxis, since, as shown by Fig. 17.21, a motile organism can also orient itself along a concentration gradient by repeated single phobic reactions. When the reaction is positive, i.e., in response to a concentration drop, this too leads finally to an approach to the chemotactic agent, just like a topotactic reaction, even if not so quickly. Examples of chemotactic orientation are the reactions of the spermatozoids of mosses and ferns to certain proteins, sugars, and to malic acid (see p. 275); an example of aerotaxis is Engelmann's bacterium experiment (Fig. 13.1B).

Instances of chemotropic bending have already been mentioned in connection with the growth of pollen tubes toward the micropyle (see p. 281) and in the discussion of the growing toward each other of the + and − hyphae (see pp. 272, 283) in the gametangiogamy of *Mucor* species. The bending of the *Drosera* tentacles (Fig. 13.1) in the middle of the leaf can occur in the direction of the captured insect, i.e., chemotropically, while the tentacles at the edges always bend toward the leaf center, which is an example of chemonasty.

Finally, many substances, e.g., amino acids (l-histidine, methylhistidine) may induce plasma currents or may accelerate them; this is known as chemodinesis, in analogy with photodinesis.

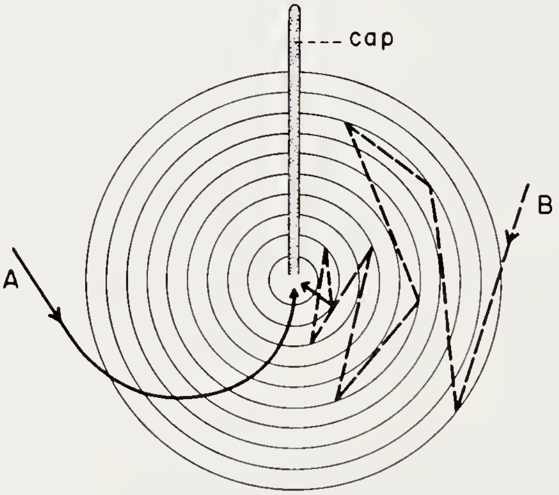

FIG. 17.21. Schematic diagram of a topic (A) and phobic (B) chemotactic orientation. cap, Capillary containing the chemotactic agent. The concentration gradient is shown by the concentric rings.

Mechanical Stimuli

Movement can also be induced by mechanical stimuli, e.g., by vibrations or by contact. Thus, bending of tendrils (cf. Fig. 17.5) is induced exclusively by contact with solid bodies (thigmotropism), while the leaf movements of *Mimosa* (see p. 368) can be induced by contact (seismonasty), injury (traumatonasty), chemical stimulation (chemonasty), or electrical stimulation (electronasty). Further examples include the movements of some stamens and stigmae induced by vibration or by contact (see p. 381 and Fig. 17.13).

In none of the cases just mentioned, which clearly demonstrate the variety of plant movements in response to various stimuli, is an exact analysis of the action of the stimuli as yet available; the various possibilities cannot, therefore, be discussed further here.

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Taxonomic Summary

Plant taxonomy is outside the scope of a textbook of general botany. Interested readers should consult relevant textbooks. However, to provide the reader of this book with at least an introductory guide the following taxonomic review classifies all the genera and species mentioned in the text into the appropriate divisions, classes, orders, and families. All orders of the subdivision Angiospermae are listed; among families, however, only those represented by at least one member in the text are given.

The basic taxonomic unit is the species. A species includes all organisms which are identical with respect to all "relevant" characteristics. The next highest unit is the genus, which consists of several related species. Several genera constitute a family, a number of families adds up to an order, several orders make a class, and a number of classes form a division. The question which characteristic is "relevant" for the incorporation of an individual into a given taxon, i.e., into a given taxonomic unit, must be decided separately in each individual case.

According to the rules of the so-called binary nomenclature all organisms are given double names; the first one written with a capital letter gives the genus while the second one, written in lower case letters designates the species. When a characteristic is common to all species in a genus, the name of the genus is often quoted on its own. The names of the families usually terminate in the ending -aceae, while those of orders end in -ales.

I. Division: Bacteriophyta
  Class: (Bacteria) Schizomycetes
    1. Order: Pseudomonadales
       Nitrosomonas, Nitrobacter, Ferrobacillus, Hydrogenomonas, Acetobacter, Azotobacter chroococcum, Rhizobium, Agrobacterium tumefaciens, Spirillum
    2. Order: Eubacteriales
       Micrococcus pyogenes var. *aureus, Gaffkya tetragena, Sarcina, Streptococcus lactis, Lactobacillus bulgaricus, L. casei, Salmonella typhosa, Escherichia coli, Clostridium pasteurianum, Cl. tetani. Bacillus subtilus, B. megaterium, Thiospirillum jenense, Chromatium, Rhodospirillum rubrum, R. molischianum*
    3. Order: Chlamydobacteriales
       Beggiatoa
    4. Order: Actinomycetales
       Streptomyces griseus, S. venezuelae
    5. Order: Myxobacteriales
    6. Order: Spirochaetales
       Treponema, Spirochaeta

II. Division: Cyanophyta
  Class: Cyanophyceae (Blue-green Algae)
  Oscillatoria chalybea

III. Division: Phycophyta
  1. Class: Euglenophyceae
     Euglena gracilis
  2. Class: Chlorophyceae (Green Algae)
     Chlamydomonas angulosa, Pandorina morum, Volvox globator, Chlorella vulgaris, Ulothrix zonata, Cladophora, Oedogonium, Valonia, Acetabularia wettsteinii, A. mediterranea, Spirogyra, Mougeotia, Zygnema
  3. Class: Charophyceae
     Chara
  4. Class: Xanthophyceae
  5. Class: Chrysophyceae
  6. Class: Diatomeae
     Pleurosigma angulatum
  7. Class: Phaeophyceae (Brown Algae)
     Cladostephus verticillatus, Dictyota, Fucus, Macrocystis pyrifera
  8. Class: Rhodophyceae (Red Algae)
     Furcellaria fastigiata, Caloglossa leprieurii, Batrachospermum

IV. Division: Mycophyta
  1. Class: Myxomycetes
  2. Class: Phycomycetes
     Phycomyces blakesleeanus, Mucor mucedo, M. ramannianus, Pilobolus
  3. Class: Eumycetes
     1. Subclass: Ascomycetes
        Saccharomyces cerevisiae, Rhodotorula rubra, Achorion schoenleini, Tricho-

phyton tonsurans, Aspergillus niger. Penicillium notatum, P. chrysogenum, Neurospora crassa, Claviceps purpurea, Gibberella fujikuroi

2. Subclass: Basidiomycetes
   Boletus edulis, B. elegans, Merulius lacrimans

Appendix Lichens
  Parmelia

V. Division: Bryophyta
  1. Class: Hepaticae
     Marchantia polymorpha
  2. Class: Musci
     Funaria hygrometrica, Splachnum ampullaceum, Fontinalis antipyretica

VI. Division: Pteridophyta
  1. Class: Psilophytinae
  2. Class: Lycopodinae
     Lycopodium, Selaginella
  3. Class: Equisetinae
     Equisetum
  4. Class: Filicinae
     Dryopteris filix-mas, Salvinia auriculata

VII. Division: Spermatophyta
  1. Subdivision: Gymnospermae
     1. Class: Pteridospermae
     2. Class: Cycadinae
     3. Class: Bennettitinae
     4. Class: Cordaitinae
     5. Class: Ginkgoinae
     6. Class: Coniferinae
        Pinus silvestris, Abies, Picea, Taxus baccata, Larix, Sequoia gigantea
     7. Class: Gnetinae
  2. Subdivision: Angiospermae
     1. Class: Monocotyledoneae
        1. Order: Helobiae (Hydrocharitales)
           Hydrocharitaceae: *Elodea canadensis*
        2. Order: Liliiflorae (Lilliales)
           Liliaceae: *Dracaena, Allium cepa, Polygonatum multiflorum, Colchicum autumnale, Ruscus hypoglossum, Bellevalia romana* (=Hyacinthus *romanus*), *Convallaria maialis*
           Hypoxidaceae: *Curculigo recurvata*
           Iridaceae: *Crocus hiemalis*
        3. Order: Cyperales
        4. Order: Farinosae (Commelinales)
        5. Order: Glumiflorae (Graminiales)
           Gramineae: *Avena, Zea mays*
        6. Order: Scitamineae (Scitaminales)
        7. Order: Gynandrae (Orchidales)
        8. Order: Spadiciflorae (Arecales)
           Palmae: *Cocos nucifera, Phoenix dactylifera*
        9. Order: Pandanales
     2. Class: Dicotyledoneae
        1. Order: Polycarpicae (Magnoliales)
           Lauraceae: *Cinnamomum camphora*

Ranunculaceae: *Ranunculus aquatilis, Delphinium, Clematis vitalba, Helleborus niger*
Berberidaceae: *Berberis vulgaris*
Nepenthaceae: *Nepenthes fusca*

2. Order: Rosales
    Crassulaceae: *Bryophyllum daigremontianum*
    Rosaceae: *Fragaria vesca, Prunus amygdalus, Crataegus*
3. Order: Hamamelidales
4. Order: Leguminosae
    Mimosaceae: *Mimosa pudica, Acacia heterophylla*
    Papillionaceae: *Robinia pseudo-acacia, Pisum sativum, Phaseolus multiflorus, Vicia faba*
5. Order: Myrtales
    Myrtaceae: *Eucalyptus globulus*
    Onagraceae: *Epilobium hirsutum, E. roseum, Fuchsia*
6. Order: Rhoeadales
    Papaveraceae: *Papaver somniferum*
    Cruciferae: *Matthiola incana, Brassica rapa, Alliaria officinalis, Sinapis alba, Nasturtium* (=*Roripa*)
7. Order: Parietales
    Cistacaea: *Helianthemum*
    Droseraceae: *Drosera rotundifolia, Dionaea muscipula*
    Violaceae: *Viola tricolor*
    Passifloraceae: *Passiflora*
    Caricaceae: *Carica papaya*
8. Order: Guttiferales
    Guttiferae: *Hypericum perforatum*
9. Order: Columniferae (Tiliales)
    Tiliaceae: *Tilia*
10. Order: Gruinales
    Oxalidaceae: *Oxalis*
    Tropaeolaceae: *Tropaeolum*
    Balsaminaceae: *Impatiens noli-tangere*
    Erythroxylaceae: *Erythroxylum coca*
11. Order: Terebinthales
    Rutaceae: *Dictamnus albus*
12. Order: Celastrales
13. Order: Rhamnales
    Vitaceae: *Vitis vinifera*
14. Order: Umbelliflorae (Umbellales)
    Araliaceae: *Hedera helix*
    Umbelliferae: *Daucus carota*
15. Order: Verticillatae (Casuarinales)
16. Order: Fagales
    Betulaceae: *Betula alba, Alnus glutinosa*
    Fagaceae: *Fagus, Quercus*
17. Order: Myricales
18. Order: Juglandales
19. Order: Salicales
    Salicaceae: *Salix, Populus*
20. Order: Piperales

21. Order: Urticales
    Ulmaceae: *Ulmus*
    Moraceae: *Ficus elastica*
    Cannabinaceae: *Cannabis*
    Urticaceae: *Urtica dioica, U. pilulifera, U. dodartii, Boehmeria nivea*
22. Order: Tricoccae (Euphorbiales)
    Euphorbiaceae: *Euphorbia, Hevea brasiliensis, Ricinus communis, Croton tiglium*
23. Order: Proteales
24. Order: Santalales
    Loranthaceae: *Viscum album*
25. Order:‘ Polygonales
26. Order: Centrospermae (Caryophyllales)
    Cactaceae: *Cereus*
    Nyctaginaceae: *Mirabilis jalapa*
    Caryophyllaceae: *Saponaria alba*
27. Order: Bicornes (Ericales)
28. Order: Primulales
29. Order: Plumbaginales
30. Order: Ebenales
31. Order: Ligustrales
    Oleaceae: *Fraxinus, Syringa vulgaris*
32. Order: Contortae (Gentianales)
    Apocynaceae: *Strophanthus, Vinca rosea*
33. Order: Tubiflorae (Polemoniales)
    Convolculaceae: *Cuscuta europaea*
    Labiatae: *Mentha piperita, Salvia, Stachys palustris, Lavandula officinalis*
34. Order: Personatae (Scrophulariales)
    Solanaceae: *Nicotiana tabacum, Hyoscyamus niger, Solanum tuberosum*
    Scrophulariaceae: *Digitalis purpurea, Antirrhinum majus*
    Plantaginaceae: *Plantago media*
35. Order: Rubiales
    Rubiaceae: *Cinchona succirubra, Coffea arabica*
36. Order: Cucurbitales
    Cucurbitaceae: *Curcubita*
37. Order: Synandrae (Asterales)
    Campanulaceae: *Campanula rapunculoides*
    Compositae: *Dahlia variabilis, Centaurea, Crepis capillaris, Taraxacum officinale, Inula helenium, Helianthus tuberosus*

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Evolution Summary

On November 21, 1859 the "Origin of Species" was published; Charles Darwin had worked on the manuscript for nearly a quarter of a century. During the voyage of the *Beagle* to South America around 1835 Darwin served as naturalist. From his observations he became convinced that species could not be separate immutable creations, but were transmutated and subject to natural selection. However, because of his background and upbringing he was very reluctant to put his ideas on paper. We owe much to his contemporaries—Hooker, Lyell, and Wallace—who contributed immeasurably to his publication.

Alfred Russell Wallace laid the foundations of zoogeography. He was the first to study adaptations and mimicry. His contributions to the species problem and his independent discovery of the principle of natural selection, submitted in a paper to the Linnean Society of London in 1858, impelled Lyell to ask Darwin to submit some notes so that he would be recognized jointly with Wallace. Lyell's book, "Principles of Geology," influenced Wallace greatly. Lyell's demonstration of slow geological change laid the groundwork for the biological evolution of Darwin and Wallace. Hooker published his "Introduction to the Australian Flora" in December, 1859 and described the descent and modification of species. In the first quarter of this century there evolved the so-called Neo-

Darwinism, in which natural selection was related to the principles of modern paleontology, genetics, and, most recently, ecology.

Although Darwin did not accept Lamarck's view on the mechanism of evolution (adaptive modifications in structure and function to environment), he did believe in the inheritance of certain acquired characters. These errors were due to total ignorance of heredity and unit character (nonblending) nature of the genetic mechanism. Organic evolution led to a study of cosmic or inorganic evolution, evolution of the universe, stellar evolution, galactic evolution, the origin of life as treated in Chapter 2, and, finally, to the question: Does life exist elsewhere?

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Evidence for Evolution

Various lines of evidence may be presented to support the theory of evolution.

GEOLOGICAL EVIDENCE—PALEONTOLOGY

Of most importance is the existence of fossils left in the rocks, such as lignites (fossil wood), petrifactions (tissues infiltrated by silica, calcium, etc.), impressions made in clay that later hardened into rock, compressions, and incrustations.

The multitudinous earth changes—erosion and deposition, elevations and subsidence, vulcanism—and the fossils correlated with them lend themselves to natural groupings or "periods." The following table shows the earth chronology and the geological distribution of plants. Note that there is a definite order in which fossil flora and fauna occurred. The lower or older strata contain the most primitive and completely extinct fossil organisms, while the higher strata contain fossils which are increasingly like those of organisms living at present.

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TAXONOMIC AND MORPHOLOGICAL EVIDENCE

Swingle (1928) summarized a number of rules or principles on which most phylogenetic systems of taxonomy are built. Studies of the external and internal structures of plants indicate that plants fall into groups of

EARTH CHRONOLOGY SHOWING THE GEOLOGIC DISTRIBUTION OF PLANTS[a]

ERA	PERIOD	CHARACTERISTIC PLANTS	GENERAL EVENTS
CENOZOIC	Recent 15,000 years ago		
QUATERNARY	PLEISTOCENE About 1,500,000 years ago	Extinction of many forms Evolution of herbs	Glaciation; rise of Man Elevation of continents
TERTIARY Mammals Flowering Plants	PLIOCENE About 15,000,000 years ago	"Cosmopolitan"	Elevation of Andes
	MIOCENE About 30,000,000 years ago	Zenith of forests distribution of	Elevation of Alps
	OLIGOCENE About 40,000,000 years ago	woody dicotyledons	Elevation of Pyrenees
	EOCENE About 60,000,000 years ago	Forests in polar regions	
MESOZOIC Reptiles Cycads Conifers	CRETACEOUS About 120,000,000 years ago	Beginnings of modern forests, but mixed with older Mesozoic types	Elevation of the Rocky Mountains Laramide revolution, Cordilleran uplift Rise of mammals
	JURASSIC About 150,000,000 years ago	Origin of dicotyledons; *Caytoniales*	Beginning of Sierra Nevada Mts. Rise of higher insects Rise of birds
	TRIASSIC About 180,000,000 years ago	Rise of Cycads and Bennettitaleans Diversification of the conifers	Rise of dinosaurs First mammals
	PERMIAN About 225,000,000 years ago	Rise of Conifers: the Voltziales	Expansion of Reptiles Elevation of Appalachians

MESOZOIC (*continued*) Amphibia Lower Tracheophytes	Carboniferous	PENNSYLVANIAN 270,000,000 years ago	Pteridosperms	Rise of Reptiles
		MISSISSIPPIAN 300,000,000 years ago	Rise of Pteridosperms	Rise of Amphibia
PALEOZOIC		(DEVONIAN) About 345,000,000 years ago	First seed-plants Rise of Lycopods, Sphenopsids, and Pteropsids Psilophytes	Age of Fish
Fish Invertebrates Algae		SILURIAN About 375,000,000 years ago	A vascular flora from Australia "First" land plants; Nematophytales	Elevation of the Scottish Highlands Age of Ostracoderms and Merastomes
		ORDOVICIAN About 435,000,000 years ago	Algae, mostly calcareous	First known fresh-water fish
		CAMBRIAN About 540,000,000 years ago	Algae, very few determinable Cuticularized spores of doubtful affinities, with tetradscars (Sweden)	Age of Trilobites First abundance of marine Invertebrates
PROTEROZOIC		"PRE-CAMBRIAN" About 1,000,000,000 years ago		Younger Laurentians
ARCHEOZOIC		About 1,500,000,000 years ago		Older Laurentians

[a] Taken from Darrah (1939).

similar forms showing marked resemblances to one another. On established morphological criteria, then, similar individuals are grouped together as a species. A number of species resemble each other so much that they are grouped as a *genus*. A number of genera stand apart as a *family*. Families are united into *orders*, orders into *classes*, and classes into *subdivisions* or *divisions* (see Taxonomic Summary).

The grouping and classification of plants is very difficult to explain except on the theory of evolutionary descent with progressive modification.

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HOMOLOGOUS AND ANALOGOUS ORGANS

The grouping and classification of plants is very difficult to explain except on the theory of evolutionary descent with progressive modification. In connection with morphological modifications, it is interesting to consider homologous and analogous organs. *Homologous* organs are similar in origin, although their functions may be different. For example, stamens and pistils are homologous structures, but vary widely in size, shape, and number. Other leaves modified as bud scales or thorns and leaflets modified as tendrils arc specific examples of homology that have evolved with time. *Analogy* in plants is seen in rhizoids (unicellular protuberances) derived from surface cells, as compared with roots (multicellular derivatives of apical meristem). While similar in function analogous organs are strikingly different in origin. Such resemblances in structure are usually described as resulting from *parallel* or *convergent evolution.*

GEOGRAPHICAL DISTRIBUTION

Most plant species, in their wild state, are not widely distributed, even though conditions favorable for their growth may be found worldwide. Such localized distribution can be explained only on the assumption that plant species evolved in the regions which they now inhabit and have been limited in their distribution by climatic, topographical, and other barriers.

Embryological Evidence

Embryology, particularly among animals, supports the hypothesis that evolutionary change has taken place. The developing individual, in passing through its complex embryonic (developmental) history, seems to repeat the adult traits of lower and thus more ancient forms. One common example of this is that the juvenile and adult leaves often differ widely in their morphology and presumably the juvenile leaves represent the ancient condition. In animals, all chordates bear a close resemblance to one another through rather late stages of development. Before a human embryo develops a real backbone, it possesses a notochord which is the adult form for the simplest chordate *Amphioxus.* The human embryo has gill slits and arterial arches suggesting those of a fish. This common beginning, followed by gradual divergence, suggests phylogenetic relationships. This theory of recapitulation is sometimes expressed in the phrase "Ontogeny recapitulates phylogeny." Ontogeny, the steps in the development of an individual as regulated by internal and external factors, has been thoroughly discussed in Chapter 16. Is it not reasonable to believe that the evolution of a species has followed a similar process?

Experimental (Genetic) Evidence

In Chapter 14 on Reproduction we saw that phenotypic variations may arise either through recombination of Mendelian factors or by mutation. The various types of corn (*Zea mays*), for example, might have been derived from a common ancestor and we may test this hypothesis by breeding experiments. Initially, different lines may have diverged through numerous chromosomal translocations, resulting in more and more sterility between the races until distinct species emerged, such as *pod* corn, *dent* corn, *sweet* corn, and *pop* corn. Extensive hybridization among distinct races, repeated hybridization with teosinte *(Euchlaena mexicana)* and perhaps also with *Tripsacum dactyloides* (Gama or Sesame grass), selection by early agricultural peoples, and particularly mutation could have produced modern corn. Mangelsdorf (1958) considers that a single mutation at the pod corn locus was more important than any other factor for determining the botanical characteristics of modern corn.

Comparative Physiology

Indications of chemical similarity or dissimilarity, based on kinds and proportions of amino acids, organic acids, sugars, etc., in species thought to be related on the basis of anatomical and other studies, confirm the concept of organic evolution (Fairbrothers and Johnson, 1961). Substances that are chemically similar are found in closely related plant species—resins and oils in gymnosperms and essential oils in the carrot, citrus, laurel, and mint families—and all further confirm the fact of evolution.

Methods of Evolution

Because of the foregoing evidence, biologists are convinced that evolutionary changes have occured and are continuing. The next question to consider is the method(s) by which organic evolution was achieved.

THE ENVIRONMENT

In Chapter 2 we considered the origin of life, tacitly assuming that conditions were very different then, than they are today. Lamarck was impressed by the effects produced by the environment. He believed that plants and animals would adapt themselves to their environment by modifying their structures and functions in such a way as to achieve adaptive changes. Structural modifications enable plants to survive in varied habitats, and the modifications permit us to recognize plants as xerophytes (dry plants), hydrophytes (water plants), mesophytes (intermediate habitat), halophytes (salt plants), etc. However, in taking exception to Lamarck, and while admitting to the possibility of some inheritance of acquired characters, biologists do not believe that an organism has the innate ability to "guide" its adaptations.

Clausen, Keck, and Hiesey (1940) explored the nature of diversity within a species in a number of plants over a period of years. Are the variations nonheritable and therefore reversible, or do they represent heritable race differences? As one example, they tested the effect of environment at stations 30, 1400, and 3050 meters above sea level in central California by the method of reciprocal transplants. The method consisted of digging an individual plant at one altitude and moving it to another elevation and, at the same time, making a reciprocal exchange in the reverse direction. The individual plant is subject to an interplay between heredity and environment. The range of modifications is always governed by the hereditary constitution of the plant. There is no tendency for lowland and upland plants to become morphologically identical when transplanted to the same garden. The dwarfing of lowland plants in the alpine region is only a superficial resemblance to alpine forms; their essential structural differences are retained. Physiological characteristics subject to change included time of breaking dormancy, the rate and duration of growth, the ability to flower, and the ripening of seed. Each climatic region is occupied by forms (ecotypes or ecospecies) particularly suited to that environment. However, the regional races are not environmental modifications, but are heritably different.

NATURAL SELECTION

Darwin's theory is stated in three parts. First, variations are continually occurring and are inherited. Second, organisms overproduce so there must be competition for survival. Third, individuals in the struggle for existence which possess any modifications in structure and function which have survival value will succeed. That is, natural selection favors survival of the fittest.

MUTATION

The Dutch botanist DeVries believed that the only variations from the normal type which led to evolutionary change were mutations. DeVries emphasized genetic variation rather than differences induced by the environment. While mutation is a most effective evolutionary mechanism, the inherited changes are small, usually lethal or disadvantageous, and may persist by hybridization even though the mutation has no selective advantage.

Alternation of Generations

The question of the alternating sporophyte and gametophyte generations is always included in discussions on the phylogeny of plants. As mentioned in Chapter 5 on Types of Organization in Plants, two somewhat different interpretations on the nature and origin of the alternating generations has been put forward. These interpretations are known as the homologous and antithetic theories of alternation of generations. The *antithetic theory* states that the gametophyte generation is the primitive one and the sporophyte is secondarily developed as an independent phase interpolated between gametophyte generations because of a delay in meiosis. The idea is developed in the text that the sporophyte generation evolved to become better adapted to a land habitat than the gametophyte. The *homologous theory,* while also recognizing the gametophyte as the more primitive, considers the sporophyte to be a modified gametophyte. Wahl (1945, 1965) in reviewing the complexity of algal life cycles considers the sporophytes to be phases in a sexual life cycle. In certain mosses and vascular plants the sporophyte can give rise to gametophytes, and gametophytes may give rise directly to sporophytes in the absence of a sexual process by *apospory* and *apogamy.* Recent studies on ferns (Wetmore *et al.*, 1964) and bryophytes (Steere, 1969) have shown that only the homologous theory fits all of the available information, and that this is now a morphogenetic problem rather than a phylogenetic one.

We may conclude our discussion of Evolution with a summary from Stebbins (1950). "Rates of evolutionary change are very diverse within different parts of an organism, between similar organisms in time, and between different groups of organisms in the same and different environments. The factors governing the rate of change are: genetic variability, the size and structure of the population, the nature of the adaptation of the population to its environment, and the rate of mutation. Within those parameters it is now possible for man to consider controlling organic evolution."

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Ecology Summary

Ecology is a word derived from the Greek "oikos" meaning "house." Because ecology is concerned with groups of organisms in a variety of environments and because man is a part of his environment and can manipulate it for good or evil, it is essential that we understand basic ecological concepts in order to conserve and to preserve our environment. In the early chapters of this volume we explored the principles of energy flow, but not in the context of an ecosystem, and carbon and nitrogen cycles, but not biogeochemical cycles and homeostatic mechanisms. We also emphasized the concept of levels of organization in dealing with protoplasm, cells, organ systems, and individual organisms. In ecology we are more concerned with populations, biotic communities, ecosystems, the biosphere, and their homeostatic mechanisms so that we may survive side-by-side with population pressure and modern technology.

We have considered many ecological (environmental) aspects of physiology, genetics, development, and evolution in the text. For this reason there is no separate chapter on "man and his environment." Rather, since ecology is such a timely and rapidly changing field, it will be left to the individual instructor and student to develop and explore such phases as they choose. A general reference list follows using suitable headings as a guide to a study of ecology.

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